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Bacteriological Studies of Freshwater Fish
II. Furunculosis in Ontario Fish in Natural Waters[1,2]

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ABSTRACT

During a period of 29 months, 1044 fish were taken from different sections of 10 streams in southern Ontario and examined for the presence of *Aeromonas salmonicida*, the bacterium causing furunculosis in fish. Most of the fish examined were brook trout (*Salvelinus fontinalis*), and carriers of furunculosis were, with one exception, found only in this species of fish. The one exception was a sculpin (*Cottus bairdi*). Most of the brook trout found to be carriers were taken from the same section of the Beaver River. As yet, no explanation can be given of the high incidence of furunculosis carriers in these waters, nor is their importance known.

INTRODUCTION

Following a survey by Evelyn and McDermott (1961) of the genera of aerobic bacteria naturally associated with several species of Ontario fish, Rabb and McDermott (1961) presented a preliminary report of the incidence of some bacterial diseases in fish in hatcheries and in natural waters of Ontario. The present paper deals only with the incidence of furunculosis in certain streams in southern Ontario and provides more detailed information on this subject than does the preliminary report.

PROCEDURE

During a period of 29 months, from June 6, 1958, to November 7, 1960, 1044 fish were taken from various sections of 10 streams in southern Ontario by means of a portable electric shocker. Most of the fish were examined bacteriologically in the laboratory as soon after catching as possible, usually the same day or the following morning after over-night refrigeration. Because of the distances involved, in a few instances fish were examined in the field employing portable equipment. Most of the fish examined were trout, but other species were included when found associated with trout. Sections of the Beaver, Credit and Nottawasaga Rivers were examined more intensively than the other streams. More brook trout (*Salvelinus fontinalis*) were examined since they were the predominant trout species in most of the streams surveyed.

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The heart, liver and kidney of each fish, and any visible lesions were all examined for the presence of *Aeromonas salmonicida*, the causative agent of furunculosis. In a few instances the spleen, ova and milt were also examined. The methods followed were those employed by Evelyn (1960), but a 2000 ppm solution of Hyamine 3500 (Rohm and Haas, Toronto, Canada) was employed instead of Iosan to swab the external surface of each fish. Bergey's Manual (1957) was used in the identification of *A. salmonicida*, and each isolate so identified was tested for pathogenicity by intramuscular inoculation into healthy brook trout. During the latter part of this survey, a chicken antiserum specific for *A. salmonicida* was found useful in identifying this organism by means of a slide agglutination test.

The fish examined were classified according to the American Fisheries Society (1960).

RESULTS

The species of fish examined from the various sections of the 10 streams surveyed are shown in Table I.

TABLE I. Fish species examined from the 6 rivers (R) and 4 creeks (C) that were surveyed.

Species	Beaver R	Big Head R	Cred t R	Ganaraska R	Mills C	North C	Nottawasaga R	Salt C	Speed R	Wilmot C	Totals
Catostomus commersoni	7	0	42	0	0	0	12	3	3	3	70
Cottus bairdi	10	0	20	0	0	2	8	0	0	9	49
Esox lucius	0	0	0	0	0	1	2	0	0	1	4
Lota lota	2	0	0	0	0	0	1	0	0	0	3
Micropterus dolomieui	0	0	1	0	0	0	0	0	1	1	3
Notropis cornutus	0	0	0	0	0	0	0	0	3	0	3
Perca flavescens	0	0	0	0	0	0	0	0	1	0	1
Rhinichthys cataractae	5	0	48	0	0	0	18	0	0	3	74
Salmo gairdneri	0	0	0	0	0	41	90	0	0	40	171
Salmo trutta	33	0	40	6	0	10	0	4	1	7	101
Salvelinus fontinalis	284	15	203	0	2	0	41	5	0	2	552
Semotilus atromaculatus	0	0	6	0	0	0	4	0	3	0	13
Totals	341	15	360	6	2	54	176	12	12	66	1044

From the 1044 fish examined, 2655 bacterial cultures were obtained. Under the cultural conditions employed, between 34 and 54% of the hearts, livers and kidneys examined from all the fish taken from the Beaver, Credit and Nottawasaga Rivers failed to show the presence of any bacteria. Between 28 and 44% of these organs showed the presence of only 1 type of bacterium per organ, while 22% or less showed the presence of 2 types, and very few the presence of 3 or more

types of bacteria per organ. These results, similar to those obtained by Evelyn and McDermott (1961), are shown in Table II. The figures for the remaining 7 streams are much the same in this regard.

TABLE II. Percentage of bacterial types isolated from hearts, livers and kidneys of all fish examined from the Beaver, Credit and Nottawasaga Rivers.

River	No. of fish examined	Organs cultured	Bacterial types isolated			
			None	One type	Two types	Three or more types
			%	%	%	%
Beaver	341	Heart	54.0	28.7	15.5	1.8
		Liver	41.4	34.0	22.0	2.6
		Kidney	36.6	42.8	19.4	1.2
Credit	360	Heart	41.4	41.2	15.4	2.0
		Liver	38.9	38.9	20.0	2.2
		Kidney	34.6	40.3	21.7	3.4
Nottawasaga	176	Heart	43.7	41.5	13.1	1.7
		Liver	34.1	44.3	21.0	0.6
		Kidney	35.2	42.6	21.0	1.2

A. salmonicida was isolated only from fish taken from the Beaver and Credit Rivers, although 833 bacterial isolates were obtained from the 343 fish, including 264 trout, taken from the other 8 streams.

From the 360 fish, including 243 trout, taken from the Credit River, 952 bacterial isolates were obtained. *A. salmonicida* was isolated from 4 of these fish, 3 brook trout and 1 sculpin (*Cottus bairdi*). No characteristic furunculosis lesions were observed on any of the fish. Two of the brook trout were among 5 two-year olds found moribund on June 16, 1958, in a section of the river experiencing a mortality of fish. The third brook trout, another two-year old, was taken dead from a different section of the river on June 5, 1959. The sculpin was taken alive from yet another section of the river on June 3, 1959.

From the 341 fish, including 317 trout, taken from the Beaver River, 820 bacterial isolates were obtained. *A. salmonicida* was isolated only from brook trout. Of the 284 brook trout examined, 37 harboured the causative agent of furunculosis, although no visible lesions associated with the disease were evident in any of the fish. All the fish carrying *A. salmonicida* were taken from Section 6 of the Beaver River, that section of the river located in Lot Number 8, Concession Number 11, Osprey Township, Grey County, Ontario. Although 2 brook trout were found dead in this section, *A. salmonicida* was not isolated from either.

Table III indicates the total number of brook trout examined from Section 6 of the Beaver River over a period of 1 year, and also the number of such trout from which *A. salmonicida* was isolated. Construction of a bridge on this section of the river prevented further observations at the time.

TABLE III. Brook trout from Section 6 of the Beaver River found harbouring *A. salmonicida* during the period Oct. 31, 1959, to Oct. 28, 1960.

Date	Water temperature		Number examined	Trout harbouring *A. salmonicida*	
	°F	°C		No.	%
Oct. 31, 1959	43	6.1	21	2	9.5
Nov. 9, 1959	40	4.4	24	0	0.0
June 9, 1960	56	13.3	16	0	0.0
Sept. 26, 1960	57	13.9	34	13	38.2
Oct. 7, 1960	50	10.0	25	5	20.0
Oct. 17, 1960	50	10.0	51	13	25.5
Oct. 28, 1960	50	10.0	32	4	12.5
Totals	...	...	203	37	...

The sex and age of the fish taken from Section 6 of the Beaver River and found to be carriers of *A. salmonicida* are shown in Table IV. The causative agent of furunculosis was isolated from 23 (20%) of the 113 male brook trout, and from 14 (16%) of the 90 female brook trout taken from this section of the Beaver River.

TABLE IV. Sex and age of brook trout from Section 6 of the Beaver River that were examined (E) and that were found carrying *A. salmonicida* (C).

	Oct. 31/59		Nov. 9/59		June 9/60		Sept. 26/60		Oct. 7/60		Oct. 17/60		Oct. 28/60		Totals	
	E	C	E	C	E	C	E	C	E	C	E	C	E	C	E	C
Males																
1	4	0	9	0	8	0	11	3	8	1	25	6	15	0	80	10
2	4	1	3	0	2	0	3	2	1	0	2	1	3	2	18	6
3	1	0	2	0	1	0	2	1	3	1	2	1	1	1	12	4
4	0	0	0	0	0	0	1	1	1	1	0	0	0	0	2	2
5	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Females																
1	6	0	8	0	4	0	12	3	5	2	16	3	8	0	59	8
2	5	1	1	0	1	0	2	1	1	0	2	2	1	0	13	4
3	1	0	0	0	0	0	2	1	5	0	4	0	3	1	15	2
4	0	0	1	0	0	0	0	0	1	0	0	0	1	0	3	0

Uncrushed ova from only 9 fish were examined. These fish were all brook trout from Section 6 of the Beaver River. *A. salmonicida* was isolated only from the ova of two of these fish, although the hearts, livers and kidneys of all nine were also examined.

The milt from only 3 fish was examined. Again, all were brook trout from Section 6 of the Beaver River. *A. salmonicida* was not isolated from the milt of

any of these fish, although it was isolated from the liver and the kidney of one of them.

Table V shows the incidence of *A. salmonicida* in the organs of the 37 brook trout from Section 6 of the Beaver River.

TABLE V. Incidence of *A. salmonicida* in the organs of the 37 brook trout from Section 6 of the Beaver River.

Organs harbouring *A. salmonicida*	Number of brook trout
Heart only	10
Liver only	9
Kidney only	8
Heart and liver	1
Heart and kidney	1
Liver and kidney	3
Heart, liver and kidney	3
Ova only	2
Total	37

DISCUSSION

The finding of the high incidence of furunculosis carriers among the brook trout of the Beaver River presents the possibility that this disease may be more prevalent than is generally realized in fish in the natural waters of Ontario.

The fish found to be carrying *A. salmonicida* in the Beaver River exhibited no characteristic symptoms of furunculosis. Others have reported apparently healthy fish to be carriers of this disease (McCraw, 1952), and the true nature of such carriers was said to be incubatory in that the infection remains latent for a variable period but eventually the disease appears in fatal form. To date, no evidence of heavy mortality of brook trout has been noted in the Beaver River.

Apparently the incidence of furunculosis carriers is not confined to any particular age-group, and probably any species of fish susceptible to the disease is a potential carrier (McCraw, 1952). The furunculosis carriers in the Beaver River were distributed fairly evenly according to age and sex, and all were brook trout. The finding of *A. salmonicida* in a sculpin from the Credit River is apparently the first report of this species of fish as a furunculosis carrier in natural waters in Canada.

While the Furunculosis Committee reported that carriers harboured *A. salmonicida* mainly in the kidney (McCraw, 1952), there was no indication of this in the Beaver River carriers. The isolation of *A. salmonicida* from the ova of Beaver River fish agrees with the reports of its isolation by others from the surfaces of eggs, and it was suggested that ova may be contaminated before extrusion if the female parent is affected (McCraw, 1952). While the causative agent of furunculosis was not isolated from the milt of the 2 Beaver River brook trout examined, Griffin (1954) reported that observations of other workers suggest that this bacterium may occur in the testes of fish.

The authors of other reports on furunculosis of fish in natural waters could not adequately explain the reason for such occurrences (Duff and Stewart, 1933; Fish, 1937; Rushton, 1936; Smith, 1960; Vickers and McClean, 1961; Wood, 1959). No explanation can yet be given for the presence of *A. salmonicida* in the brook trout from the Beaver and Credit Rivers. Brook trout yearlings were planted in the Beaver River near Section 6 in the spring of 1959 and the spring of 1960, but these fish had no known history of furunculosis. While the opinion exists that furunculosis may become established among wild fish through the planting of infected fish (McCraw, 1952), very little is actually known about the importance and fate of such fish in natural waters. Belding (1927) claimed that diseased fish are less dangerous when stocking occurs in widely separated waters where the fish would tend to die without infecting others. Fish (1937) stated that so little is known about furunculosis as it may exist outside the hatcheries that few facts are available on which to base a conclusion as to how much actual damage has been or is being done to the trout resources by liberating furunculosis-infected fish. Rucker *et al.* (1954) felt that in salmon furunculosis is often self-limiting, for in a number of instances the disease had disappeared from controls which were not given sulfonamide treatment.

The incidence and the importance in natural waters of fish harbouring *A. salmonicida* is still unknown. According to Davis (1944), the popular conception that hatchery fish more often suffer from infectious diseases than do wild fish is erroneous and based on inaccurate and fragmentary information. The authors agree with Davis (1944) that "there is probably no field of fishery research which promises more for the effort expended than a study of the diseases of our wild fishes."

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Glycogen Concentration and Post Mortem Loss of Adenosine Triphosphate in Fish and Mammalian Skeletal Muscle. A Review[1]

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During the past few years a great deal of interest has been shown in the biochemical changes that accompany rigor mortis in fish muscle. This brief review is confined to certain aspects of the findings that have been made, particularly regarding glycogen and adenosine triphosphate (ATP) and, to a lesser extent, creatine phosphate; to a comparison of these findings with those from similar investigations made with mammals; and to a discussion of possible reasons for differences between the findings of different investigators.

In mammalian skeletal muscle it has been found that the ATP concentration (measured as acid-labile phosphorus (ALP)) may, under certain circumstances, be maintained with little or no loss for periods of time varying between a few minutes and several hours post mortem (e.g. Bate-Smith and Bendall, 1947; Marsh, 1952; Lawrie, 1953; Marsh, 1954; Partmann, 1961; Briskey and Wismer-Pedersen, 1961). In fish skeletal muscle, on the other hand, it appears to have been the usual experience that ATP (measured either specifically as ATP or less specifically as ALP) decreased more or less rapidly from the time of killing (Fujimaki and Kojo, 1953; Heen, 1954; Saito and Hidaka, 1955; Noguchi and Yamamoto, 1955a; Asakawa, 1957; Saito and Arai, 1957; Saito *et al.*, 1959; Nakano and Tsuchiya, 1960; Partmann, 1960; Suyama *et al.*, 1960; Jones and Murray, 1961; Fraser *et al.*, 1961; Nagayama, 1961). Recently, however, several instances have been reported in which ALP remained at a high concentration for several hours post mortem in the muscles of some species of fish killed in an unexercised condition (Nakano and Tsuchiya, 1960; Nakano, 1961; Partmann, 1961; Tomlinson *et al.*, 1961). The effect was not observed in certain of these species killed in an exercised or exhausted condition (Tomlinson *et al.*, 1961). It is possible that Fujimaki and Kojo (1953) observed the phenomenon in part of their work some years ago, although this is not certain. In a few other instances, the periods of time elapsed between first and second measurements post mortem, together with the small losses of ATP or ALP observed, suggest that if measurements had been made at shorter intervals, maintenance for some time at the initial concentration would perhaps have been found to occur (Saito and Arai, 1957 (see below); Partmann, 1960; Fraser *et al.*, 1961). The work of Partmann (1961) in particular has shown that in rainbow trout (*Salmo irideus*

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Gibb) and mirror carp (*Cyprinus carpio* L.) muscle ALP concentration can be maintained post mortem for periods of time comparable to those in mammalian or avian muscle. Partmann found, however, that in fish muscle brei (at 5°C) loss of ALP was very much more rapid than in intact muscle or in beef muscle brei, and was also very much more rapid in thawing frozen fish muscle than in thawing beef muscle. Saito and Arai (1957) and Partmann (1961) have also shown that destruction of ATP in fish muscle proceeds much more rapidly at temperatures between –2 and –4°, or a little lower, than at temperatures above or below this range. Such an effect was not found in beef or chicken muscle (Partmann, 1961).

In reporting some very interesting findings regarding the course of degradation of nucleotides in relation to rigor mortis in cod (*Gadus callarias*) muscle, Jones and Murray (1961) suggested that the observed absence of maintenance of ATP concentration in the muscle of those fish post mortem, in contrast to that observed in mammalian muscle, reflected the low glycogen concentration available for glycolysis in fish muscle. While low glycogen concentration at death may have been the reason for lack of maintenance in cod muscle, and although the opinion that fish muscle is low in glycogen in comparison with mammalian muscle seems to be rather widely accepted, evidence is accumulating that indicates a generalization of this nature should be regarded with caution.

Part of the data on which such a view is based have been obtained with fish that had been treated in some manner that might be expected to result in a reduction of their muscle glycogen; with young or small fish; or with fish that were not eating for various reasons. This is not a criticism of the work that has been done, for in much of it the measurement of muscle glycogen was incidental to some other objective, but these facts should be taken into account in the present context. Thus, MacLeod and Simpson (1927) determined glycogen and lactic acid in the muscles of fish caught by hand line or trawl, and the values recorded for glycogen were low; for example they ranged from 0.04 to 0.48% in the muscle of hand-lined haddock. At the same time, however, values for lactic acid ranged from 0.24 to 0.48% in the muscle of these haddock and suggest a loss of glycogen during the struggle involved in catching and killing. Since Black *et al.* (1961) have shown that in relatively short periods of severe exercise formation of muscle lactate is inversely correlated with the decrease in muscle glycogen, these data indicate an actual glycogen content in unexercised haddock muscle of the order of 0.4 to 0.7%. Root *et al.* (1931), in the course of a study of the influence of insulin injections on glycogen distribution in the scup (*Stenotomus chrysops* L.), determined glycogen in the muscles of fish weighing about 250 g that had been taken from commercial traps or caught by hook and line and then held 24 hours in running sea water. These fish were exsanguinated before being killed, and muscle glycogen was found to be 0.088%. Miller *et al.* (1959) measured the muscle glycogen in unexercised rainbow trout (of average weight 71 g) killed immediately after a blood sample was withdrawn by cardiac puncture, and found it to be 0.178 ± 0.079% or 0.118 ± 0.021% depending on the diet fed. In each of these last two investigations the fish used were small and

their treatment prior to sampling could be expected to lead to some reduction of their muscle glycogen. In particular, recent findings by Black *et al.* (1962) regarding the slow replacement of fish muscle glycogen following exercise indicate that the value for glycogen in the scup would represent only a fraction of that present in the muscle before the capture of the fish. Tarr (1950) used fish weighing 50 to 200 g in a study primarily concerned with acid-soluble phosphorus compounds of the muscle. He pointed out that the values for glycogen recorded (0.023 to 0.113%) were low and suggested that this may have been due to a poor nutritional condition. Black *et al.* (1960) were interested in the changes, including those in muscle glycogen, that would be brought about by exercise. Two groups of fish were studied. In one the mean weight of the fish was 68 g, in the other it was 540 g. In the first group of 10 fish, muscle glycogen was found to range between 0.01 and 0.171% (mean 0.085%), while in the second group, which was said to be in spawning condition and therefore not feeding, values ranged between 0.032 and 1.9% (mean 0.378%). In connection with this last and other work Black *et al.* (1961) have pointed out that there is evidence to suggest that muscle glycogen levels are higher in mature than in immature fish. These examples illustrate the point being made. Black *et al.* (1961) have considered in detail the difficulties encountered in interpreting the data of investigations relating to glycogen content.

Values for muscle glycogen in relatively well-grown fish in an unexercised, feeding condition are not numerous, but there are some data of this nature. Dill (1921) reported values of 0.5, 0.22 and 0.17% in three determinations for what were described as live sardines. MacPherson (1932) reported values of 0.44 to 0.64% for haddock, and Sharp (1934) found values of 0.6 to 0.85% for the same species. Amano *et al.* (1953) reported 0.6% in hand-lined mackerel immediately killed on landing by severing the motor nerve. In these fish considerable differences were found in glycogen content between different portions of the muscle (range 0.38 to 0.65% in one fish), and in all the fish examined the glycogen content decreased and lactate increased very markedly depending on the method and rapidity of killing after capture. If glycogen and lactate are considered together (see above) they suggest glycogen values in the unexercised mackerel ranging from about 0.59 to 1.08%. Noguchi and Yamamoto (1955b) recorded values of 1% in red snapper, 2.5% in mackerel and 2.3% in carp immediately decapitated on catching. Jones (personal communication) found 0.2 to 0.6% glycogen in the muscle of cod. Very recently, Hochachka and Sinclair (1962) reported that the glycogen concentration of the epaxial muscle of small rainbow trout was raised to a value 8 to 9 times higher than that usually observed (about 1.5% instead of the usual 0.17%) as a result of heavy feeding. Thus, although the muscles of small fish have usually been found to contain low reserves of glycogen, these, as Hochachka and Sinclair point out, are influenced by nutrition, and therefore are not necessarily characterictic of such fish. In elasmobranchs, Suyama *et al.* (1960) found 0.099 to 0.228% glycogen in the muscle of skate (*Dasyatis akajei*) and 0.396 to 0.631% in shark (*Triachis scyllium*).

As far as we are aware, glycogen values are not available for tuna, but Tsuchiya and Kunii (1960) have reported accumulation of lactic acid to the extent of 1.1 to 1.2% in muscle post mortem, and we have found similar values (Tomlinson *et al.*, 1962). Tsuchiya and Kunii reported a wide range of values for lactic acid in the white muscle of other species, varying from a low of 0.03% in flatfish through values such as 0.14 to 0.27%, respectively, in Alaska codfish and carp, to 0.49 to 0.69% in sardines. The nutritional condition of the fish used in this work was not known. In trout, flounder and sockeye salmon killed unexercised or as quickly as possible after landing we found maximum accumulation of lactic acid of 0.6 to 0.7%, about 0.3%, and 0.8 to 1.0%, respectively (Tomlinson *et al.*, 1961).

In mammals, Hamoir (1961) lists a range for muscle glycogen of 0.5 to 1.0% with particular values for ox of 1.1%, sheep 0.7%, rabbit 0.8 to 1.5%, white rat 0.33 to 0.54%, seal 0.7 to 1.3%, and dolphin (starved 24 hours) 0.98%. According to MacLeod and Simpson (1927) values for decapitated cats range between 0.3 and 0.7%; Bate-Smith and Bendall (1956) found 0.79 $\pm$ 0.03% in the psoas muscle of well-fed rabbits anaesthetized before being killed, and 0.25 to 0.34% in that of animals beheaded without anaesthesia. Briskey and Wismer-Pederson (1961) reported glycogen content in pork muscle ranging from about 0.4 to 0.8%, with about 0.6 to 0.8% lactic acid present in the muscle at the same time. Maximum lactic acid accumulation in pork reached about 1.0 to 1.4%.

Few as the data are for fish, a careful comparison with those for mammals leads to the conclusion that while many fish may usually have muscle glycogen concentrations somewhat lower than those found in mammals, the concentrations in others fall well within the range reported for mammals.

In considering reasons why some investigators have observed immediate, relatively rapid loss of ATP (ALP) from fish muscle while others have observed no loss for the first few hours post mortem, it appears that while muscle glycogen concentration at death is no doubt important, other factors are also concerned. It has been observed (Briskey and Wismer-Pederson, 1961) that a rapid loss of ALP can occur in pork muscle with high glycogen concentration at death, whereas in that from another pig with comparable or even lower glycogen reserves, ALP may persist at a high concentration for several hours post mortem. The reason for this difference does not seem to be clearly understood although Briskey and Wismer-Pederson have suggested that certain chemical and chilling rate differences between muscles may be the cause. There appears to be some relation between the findings of Briskey and Wismer-Pederson and those of Lawrie (1953) which demonstrated that there are differences between myoglobin-rich and myoglobin-poor muscles in their ability to maintain energy-rich phosphate (ALP) concentration post mortem. The circumstances under which an animal is killed can have a remarkable effect on glycogen reserves, on phosphocreatine and on the course of loss of ALP from muscle post mortem. Bate-Smith and Bendall (1956) have presented this effect very clearly. They compared two groups of rabbits, both well-fed, one of which was killed under anaesthesia (quiet death), the other being stunned by a blow on the head and then beheaded (violent

death). Glycogen decreased by more than 50% during killing in the "violent death" group in comparison with the other (see paragraph on mammalian glycogen above). Phosphocreatine was destroyed during killing and ALP decreased from the time of killing in the "violent death" group, while in the other group phosphocreatine was at a fairly high concentration in the muscles after death and ALP concentration did not decrease for several hours post mortem. Also in this work Bate-Smith and Bendall showed that the difference in glycogen content of muscle after killing was not alone responsible for the difference in rate of loss of ALP post mortem, for in a third group of animals, that were starved for 48 hours then killed under anaesthesia, ALP concentration was maintained for several hours post mortem although the initial glycogen content of the muscle was only 0.32%. In this third group phosphocreatine was at a high concentration after killing. Bate-Smith and Bendall concluded that glycogen and phosphocreatine each had a role in the maintenance of ATP post mortem. It is noteworthy that in both our work (Tomlinson *et al.*, 1961) and that of Nakano (1961) phosphocreatine was usually at a fairly high concentration at death in the muscles of those fish in which ALP remained at a high concentration for some hours post mortem. Amano *et al.* (1953) found that killing frigate mackerel (*Auxis tapeinosoma*, Bleeker) by severing the motor nerve resulted in a smaller loss of muscle glycogen during killing than did beheading, and that subsequently glycogen disappearance and lactic acid formation proceeded more slowly in the fish killed by puncturing the nerve. It is known that the degree of handling to which fish muscle is subjected greatly influences the course of rigor mortis and presumably the biochemical changes that accompany it (Partmann, 1960; Dyer and Fraser, 1961; cf. de Fremery and Pool, 1960, in which it is shown that ALP and pH both decrease more rapidly post mortem in beaten than in control chicken muscle). The effect of storage temperature is well known, and it was demonstrated some time ago that availability of oxygen can exert a marked influence on the course of rigor mortis in rabbit muscle (Fletcher and Hopkins, 1917). It has been found that a similar effect — a slowing of the rigor process by increased oxygen tension — occurs in fish muscle (H. Buttkus, personal communication). Lawrie (1953) observed that ALP decreased more slowly in mammalian muscle post mortem under aerobic than it did under anaerobic conditions. It seems possible that fear induced in fish prior to killing might have some influence on results, for adrenaline is known to exert a powerful influence on utilization of glycogen in mammalian muscle (Cori and Cori, 1928; Radouco-Thomas *et al.*, 1959), and may interact with relaxing substance to influence the strength of muscular contraction (Stam and Honig, 1962). There is evidence indicating that antemortem subcutaneous injection of adrenaline may hasten onset of rigor mortis (Sacks, 1927). In fish, while there is some uncertainty regarding the effects of adrenaline in comparison with those found in mammals (Hoar, 1957), MacKay (1931) has shown that it exerts a long continued pressor action in the skate, and McCormick and MacLeod (1925) found its hyperglycemic activity to be similar to that in mammals. On the other hand, adrenaline has not yet been shown to influence the formation of cyclic adenosine-3′, 5′-phosphate (a nucleo-

tide, one of whose functions is related to muscle phosphorylase activity) in fish, although it does so in many mammalian tissues (Sutherland and Rall, 1960). The enzyme or enzyme system concerned in this action of adrenaline, adenyl cyclase, however, has been shown to be present in at least one species of fish (Sutherland *et al.*, 1962). In addition to these possible variables, different species of fish were used in many of the investigations. This did not always occur, however, so that in some instances different results have been obtained by different investigators working with the same species (e.g. Saito *et al.* (1959) and Tomlinson *et al.* (1961), with rainbow trout (*S. gairdnerii*); Saito and Hidaka (1955), Noguchi and Yamamoto (1955a), Saito and Arai (1957), and Partmann (1961), with carp (*Cyprinus carpio*, L.)). In carp, although the first three groups of workers recorded losses of ALP or ATP between the first and second measurements, those recorded by Saito and Arai (for ATP) were very small, being about 13% at 16°C in 2 hours and 7% at 0°C in 8 hours. Although different storage temperatures and different methods of killing and post mortem treatment of muscle may have been at least partly responsible for some of the differences observed (e.g. Saito *et al.* (1959) killed their trout by beheading and skinned and filleted them before they were sampled and stored, whereas Tomlinson *et al.* (1961) killed their fish by a heavy blow on the head and stored them in the round) it does not seem to be possible at present to ascribe the differences between results of different investigations with certainty to any of the possible causes discussed.

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Relation Between Water Temperature and Gastric Digestion of Largemouth Bass (*Micropterus salmoides* Lacépède)[1]

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ABSTRACT

The rate of gastric digestion of largemouth bass (*Micropterus salmoides* Lacépède) was measured at 5, 10, 15, 20 and 25°C temperature by the X-ray method of the authors. Bleak (*Alburnus alburnus* L.) of 8.0–8.5 cm length were force-fed to largemouth bass of 25–27 cm length. There was a more rapid increase in the rate of digestion in the range between 5° and 10° than at higher temperatures. In the stomach of bass the food fish was rolled up into the shape of a spiral during digestion. Because these measurements, unlike *in vitro* experiments, were made under circumstances similar to those existing in nature, they may serve as an indication of rate of digestion in the wild.

INTRODUCTION

In the course of experiments dealing with the digestion of predatory fishes living in central Europe at first the relationship between rate of digestion and temperature was investigated. Two foreign fish species the largemouth bass (*Micropterus salmoides* Lacépède) and a catfish (*Ameiurus nebulosus* Le Sueur) were studied, besides some native Hungarian fishes. It was suggested that by studying these two acclimatized species valuable comparative data would be obtained, for they belong to families (Centrarchidae, Ameiuridae) which are far removed systematically from our indigenous predacious fishes (Percidae, Siluridae, Esocidae). The results of experiments performed with largemouth bass are presented in this paper.

The largemouth bass has great economic importance in Hungary as a subsidiary fish in carp fish-ponds. Its voraciousness makes it a valuable helpmate of both pike-perch and catfish in eating up noxious coarse fish. Nevertheless, the largemouth bass has not proliferated widely in our natural waters since its acclimatization early in the twentieth century.

Our studies of the relationship between duration of gastric digestion of predacious fishes and water temperature were started on pike-perch (*Lucioperca lucioperca* L.—Percidae). An X-ray method was designed to follow the process of gastric digestion (Molnár and Tölg, 1960, 1962).

These experiments were necessitated by the food studies (analysis of stomach contents) carried out on the natural population of pike-perch in Lake Balaton, because for further investigations it was necessary to establish the seasonal

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changes in the rate of gastric digestion, and to determine the digestive capacity of pike-perch at different water temperatures, in order to assess on this basis the quantitative changes in its food at different seasons. On the basis of investigations of the relation between enzyme activity and temperature published in fish-biological literature (Kostojanc and Korjujev, 1934; Schlottke, 1940; Jancarik, 1949; Kashiwada, 1952; Ananicsev, 1959), no opinion could be formed concerning seasonal changes in the rate of digestion of pike-perch under natural conditions.

Similar problems have been raised by some American authors (Brown, 1946; Baldwin, 1957; Podoliak, 1961). Moreover there are many who have dealt with the relation between metabolism and temperature in largemouth bass (Markus, 1932; Kramer and Smith, 1960; Strawn, 1961); hence it was thought that these studies would be of interest also to American specialists.

The measurement of activity of gastric juice by *in vivo* experiments seems to be a new effort in fish biology. By coupling these data with the present physiological knowledge of the fish species investigated, a more complete picture may be obtained of the process of digestion. These experiments were run under conditions similar to natural conditions, therefore not only may physiological inferences be drawn from them, but also fishery-biological and limnological conclusions. In evaluating these findings made on the digestion of bass we have used the physiological results by Sarbahi (1951), Winberg (1960) and Podoliak (1961), and the references pertaining to fishery biology by Markus (1932), Bennet (1937), McLane (1948), Padfield (1951), Schneidermeyer and Lewis (1956), Kramer and Smith (1960, 1962), Lewis *et al.* (1961), Strawn (1961) and Maloney *et al.* (1962).

These experimental data pertaining to the changes of the rate of digestion should be useful to workers studying the biology of largemouth bass.

MATERIAL AND METHODS

The experiments were performed with 3-year-old bass of standard length 25–27 cm each, raised in a hatchery pond. The fish were held in aquaria through which natural lake water flowed. The water in these through-flow type aquaria was also aerated. Ten experimental largemouth bass were placed into each aquarium, containing 140 liters of water.

At the start of the experiment bleak (*Alburnus alburnus* L.—Cyprinidae) of 8–8.5 cm length were force-fed to largemouth bass. The fish received one bleak each.

The experiments were carried out at 5, 10, 15, 20 and 25° C temperatures. The process of digestion was observed by the X-ray method mentioned above. The essence of the method is that in predacious fishes having a stomach the food fish, when fed whole, gives a definite shadow on an X-ray film. During digestion the skeleton of the food fish is softened, and the shadow on the X-ray film becomes gradually more indefinite and finally disappears. The disappearance of the shadow of the stomach content indicates the end of gastric digestion and also the emptiness of the stomach (Molnár and Tölg, 1960).

The experiments at low temperatures (5°, 10°) were carried out in winter, those performed in warm water (20°, 25°) in summer, and the experiments at 15° in the autumn. The fish used were taken from their habitat 3–4 weeks before the experiments. At the start of the experiments they were feeding voluntarily, thus it may be presumed that they had got used to captivity.

The aquaria of the Biological Institute at Tihany are fed from Lake Balaton itself. In the course of a year the temperature of the water in the aquaria varied between 5° and 23.5°C in temperature. Experimental work was greatly facilitated by these fundamentals. The temperature in the experimental aquaria was adjusted by an intermediate aquarium regulated with an ultrathermostat. Into this aquarium was fed the fresh water of the lake, where it was heated to 1–3 degrees higher temperature. From there lake water thus adjusted to the temperature required was let into the experimental container. By this procedure it was possible to maintain constant temperature during the experiment, furthermore the experimental fish were kept in flowing water. Acclimation to the temperature in question was started 4 days before the experiment.

During these investigations all factors, including the length of both the largemouth bass and the food fish employed, were the same, except for temperature.

Ten largemouth bass were used at each temperature. The experimental fish were tagged beneath the dorsal fin, the food fish were marked by varied clipping of the caudal fin. Vomiting occurred only seldom, and with this double marking it was possible to identify the food fish leaving the stomach and to shove it back again into the empty largemouth bass to which it belonged.

During radiography bass were narcotized in a 2-methylchinoline (Quinaldin) solution at a dilution of 1:50,000 (Muench, 1958). By this treatment the fish lay immobile on the film-holder. The fish put back into the aquarium after photography recovered from their narcosis in a few minutes. Rate of digestion, as shown by control experiments, was not affected by narcosis.

The radiographs of different fish were taken at different intervals, depending on temperature. They show both the softening action of the stomach, and the changes of position of the stomach contents.

RESULTS AND DISCUSSION

Average values of the data of time of digestion and their standard deviation are given at each temperature in Table I, and are plotted in Fig. 1.

TABLE I. Rate of gastric digestion of largemouth bass of 25–27 cm standard length, force-fed with one bleak of 8–8.5 cm length.

Temperature, °C	5°	10°	15°	20°	25°
Time of emptying of stomach (*hours*)	110	50	37	24	19
Standard deviation (*hours*)	12.90	6.87	8.29	4.22	2.21

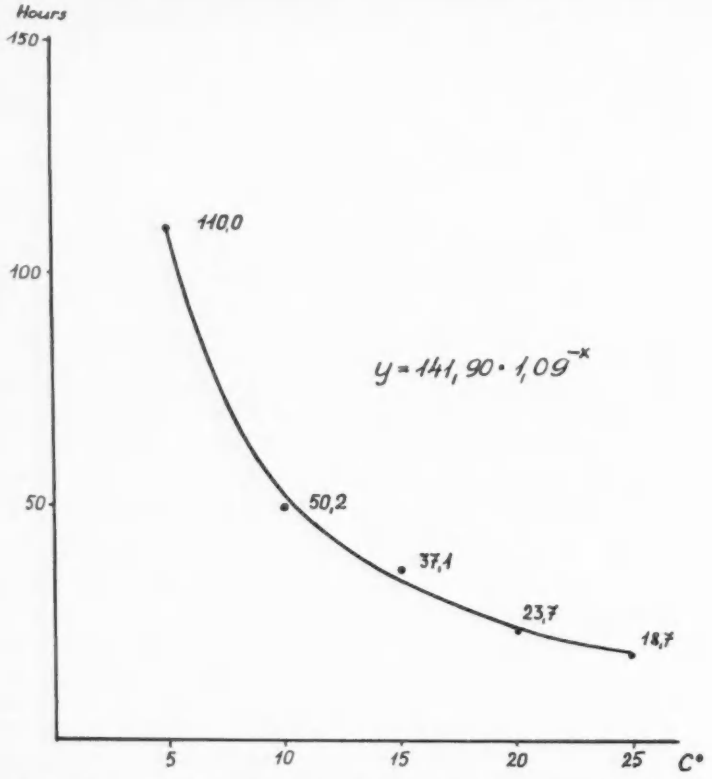

FIG. 1. Change in the intensity of gastric digestion of largemouth bass between 5° and 25°C. The great increase of intensity between 5° and 10° is most conspicuous.

According to these data there is a rapid increase in the intensity of digestion in the range 5–10°C. The increase is not so large at temperatures above 10°.

These findings are more striking when the data are expressed in percentages. If the duration of emptying of stomach at 5° (110 hours) is taken as 100%, the averages will be 45.6% at 10°, 33.73% at 15°, 21.54% at 20° and 17.0% at 25°, respectively. From these percentage figures, a rise of temperature from 5° to 10° resulted in more than 50% increase in rate of digestion, whereas at 25° the duration of digestion decreased by only 28% in comparison with 10°C.

Plotting the mean values of time of digestion against temperature on a logarithmic scale on both axes, the points lie along a straight line (Fig. 2). Thus there is a linear relationship between the logarithm of time of digestion of largemouth bass and the logarithm of the corresponding temperature. Using this graph, it is possible to determine with approximate accuracy the velocity of digestion at any temperature at which no experiments were performed, namely

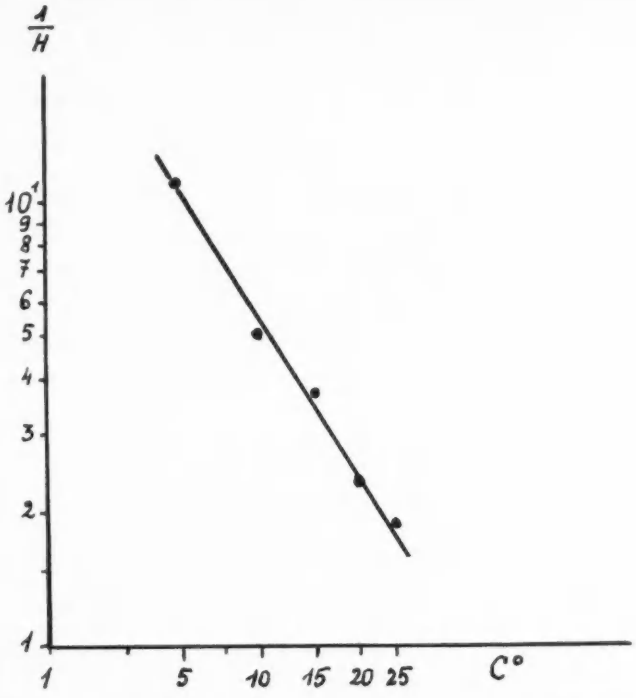

FIG. 2. A straight line describes the increase in rate of gastric digestion of largemouth bass as a function of temperature, on a double-logarithmic plot.

at any intervening point between 5° and 25°. Also, extrapolation can be made to temperatures below 5° and above 25°, which are lethal for largemouth bass.

In our previous studies, performed with pike-perch, there was a linear relation only between the logarithms of the rates of digestion and actual temperature values, that is, a semilogarithmic relationship (Molnár and Tölg, 1962). Comparison of these results with our present findings shows that with increasing temperature the increase in rate of digestion is more conspicuous in largemouth bass than in pike-perch.

The radiographs show that the stomach content of the largemouth bass is rolled into a spiral shape during digestion (Plates 3–5), which phenomenon was not observed in the case of pike-perch. The food fish in the stomach of the bass is bent, generally even at the beginning of digestion (following the dorso-ventral inflexion of stomach) and subsequently it takes on more definitely a shape resembling an "anchovy ring". The stomach contents are moved about with considerable force. The observation that the stomach, as its shape varies, occasionally dents the turgid wall of the swimbladder is also indicative of

this (Plate 6). It is most likely, also, that the motion of the stomach contents increases the rate of digestion. In the case of pike-perch, however, contrary to these observations, the food fish remains immobile in the stomach, lying parallel with the axis of the spine in the same position as it was artificially placed into the stomach. Consequently, in this fish there is no stimulating effect of motion of the stomach.

STATISTICAL ESTIMATION OF THE EXPERIMENTS

The values obtained were subjected to variance analysis (Snedecor, 1957). The results of computations are presented in Table II.

TABLE II. Analysis of variance of experimental data.

Source of variation	Sum of squares	Degrees of freedom	Mean squares
Temperature	54166.3	4	13541.57**
Repetition	501.0	9	55.67
Error	2243.7	36	62.32
Total:	56911.0	49	

**Significant at $P<1\%$.

It is seen from the mean squares given in Table II that the differences between data obtained are due decisively to the factor investigated—temperature. The sum of squares for error, 2243.7, is negligible beside the effect of temperature, 54166.3.

TABLE III. Differences between treatment means and least significant difference.

Temp., °C	5°	10°	15°	20°	Least significant differences:
25°	91.3	31.5	18.4	5	
20°	86.3	26.5	13.4		P=5%: 7.17 hours
15°	72.9	13.7			P=1%: 9.60 "
10°	59.8				P=0.1%: 12.67 "

Table III shows that there is no difference between treatment means at 20° and 25°. Between all other treatment means, however, there is difference at the 0.1% level. The failure to demonstrate a significant difference between the means at the two highest temperatures does not reduce the value of the experiments for it indicates that at similarly high temperatures it would be difficult to prove statistical differences in the intensity of gastric digestion in the case of largemouth bass.

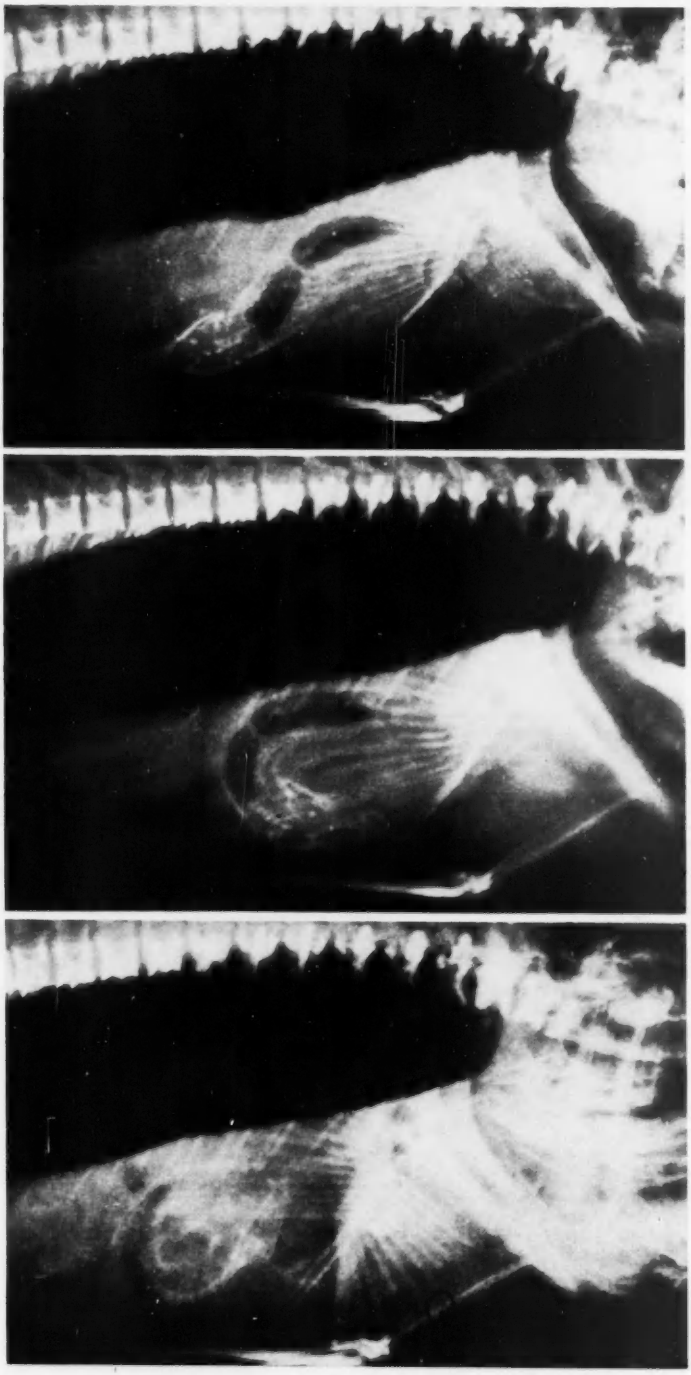

FIG. 3. **Top:** General view immediately after force-feeding. The axis of the full stomach is at an angle to the direction of the spine. **Middle:** The stomach content is curved at the start of digestion. **Bottom:** At an advanced state of digestion, the food fish becomes gradually rolled up into the shape of a ring, insofar as softening of its muscles allows.

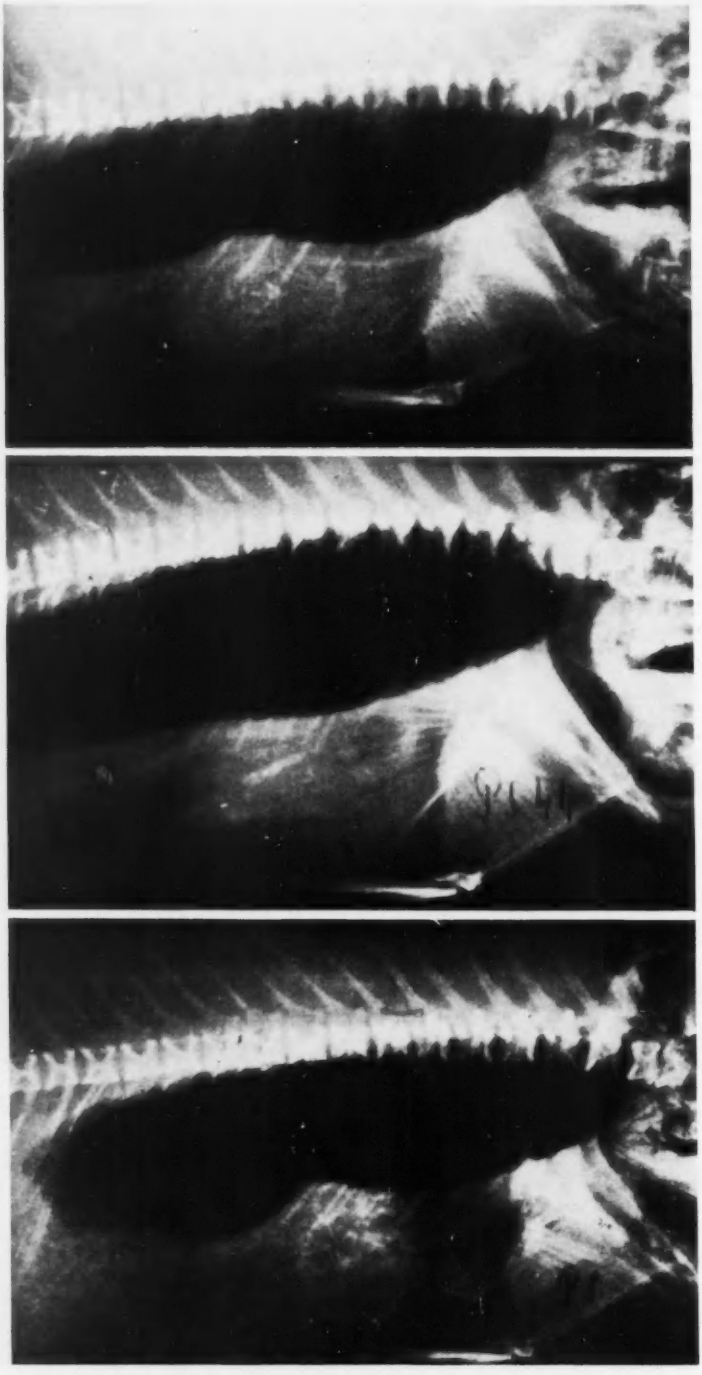

FIG. 4. **Top:** Toward the end of digestion the food fish becomes rolled up like an "anchovy ring". **Middle:** A piece of the spine, only a few centimeters in length, indicates the end of digestion. **Bottom:** The turgid swimbladder occasionally becomes dented, indicating the energy with which the stomach contents are moved around.

CONCLUSIONS FOR FISHERY RESEARCH

Inasmuch as these experiments were carried out seasonally and at temperatures characteristic for the period of time in question, and because before the start of the experiments the fish were kept at the temperatures prevailing in their natural habitats, it is suggested that these findings reflect also seasonal changes in the intensity of digestion. The data show that considerable differences may be experienced in this respect. On the basis of results obtained at 5° and 25° it may be concluded that the rate of emptying of the stomach is 5–6 times slower in winter than in summer. This means a similar difference in rate of feeding. In view of these essential differences, the results of analyses of stomach contents performed in summer and in winter are not directly comparable. A food supply is more valuable in summer, from the point of view of the fish population, because it is more intensively utilized by largemouth bass in this season than in winter.

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The Occurrence of the Longjaw Cisco, *Leucichthys alpenae*, in Lake Erie[1]

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ABSTRACT

The longjaw cisco, *Leucichthys alpenae*, is shown to be a species new to the Lake Erie fauna. The taxonomic work on Lake Erie ciscoes is reviewed. Thirty three specimens of *L. alpenae* taken in 1946, 1947 and 1957 are compared morphometrically with *Leucichthys artedi* of Lake Erie, the only other cisco species in the lake. *L. alpenae* has a longer and deeper head, longer maxillary and fewer gill rakers. *L. alpenae* is more distinct from *L. artedi* in Lake Huron than in Lake Erie. The rate of growth of *L. alpenae* in Lake Erie compares favourably with that in Lake Michigan.

New distribution records of species endemic to the Great Lakes are rare. It is not too surprising, however, that such a discovery should occur among the coregonids—the most abundantly represented family in the Great Lakes and one comprised of fish of apparently such recent origin (Smith, 1957) that the species are difficult to describe, and often even more difficult to recognize for the untrained observer.

A recent new record was based on the discovery of the pygmy whitefish, *Prosopium coulteri*, in Lake Superior in 1952 (Eschmeyer and Bailey, 1955). Its small size, and occurrence in depths of 10–50 fathoms, contributed to the absence of this species from commercial gill and impounding nets designed to capture only large fish, and from the shore seines employed in fishery surveys. Some individuals may have been taken in small-mesh gill nets used to catch bait for lake trout hooks, or in seines hauled for lake herring, but to the untrained eye of the fisherman they may have appeared to be only young of their closest relative, *Prosopium cylindraceum*.

Circumstances were similar in the recent discovery of the shortnose cisco, *Leucichthys reighardi*, in Lake Huron[2] and longjaw cisco, *L. alpenae*, in Lake Erie. Both of these species undoubtedly have been taken by commercial fishermen but in small numbers for they are most common in areas seldom fished with

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[2]The first record of the shortnose cisco in Lake Huron was made by biologists of the research vessel *Cisco* during a general fishery survey by the U. S. Bureau of Commercial Fisheries of Saginaw Bay and southern Lake Huron in 1956.

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gear best suited for their capture. Indeed, the fishermen at Port Dover, Ontario, have long been aware of the presence of a deepwater cisco in the "deep hole" of eastern Lake Erie. They were poorly represented in commercial landings, however, because they were not taken in abundance except near the spawning time, which occurred during the stormy period in November and December, and fishermen were reluctant to fish far from shore for uncertain catches of a fish for which there was no firm market. The gross similarity of these fish to the shallow-water cisco or lake herring (*L. artedi*), the only other cisco in Lake Erie, hindered their clear recognition as anything truly different by the fishermen, or by biologists who may have examined catches of lake herring in which one or a few deep-water forms may have been present. Difficulties of recognition under such circumstances would be even greater in Lake Erie than in other lakes because the lake herring, the most variable member of its genus (Koelz, 1929), has displayed a wider variation of forms in Lake Erie than in any other single body of water. So diverse are the forms of lake herring there that this single species has been at times described as at least six species (Dymond, 1922).

The longjaw cisco (*L. alpenae*) in Lake Erie was first recognized positively during a study of the Lake Erie cisco (lake herring) during 1945–49 sponsored by the Ontario Department of Lands and Forests and the Research Council of Ontario (Scott, 1951). Commercial catches at Port Dover in 1946 produced 6 specimens that seemed to stand conspicuously apart from the hundreds of other ciscoes examined because of their broader back and heavier head and head parts. Another such specimen was located among ciscoes landed at Erieau in 1947. Closer examination of these fish revealed gill-raker counts ranging from 30 to 34, decidedly below the counts of 37–53 for 1,300 shallow-water ciscoes taken during the same period (Scott, 1950). These fish most closely resembled *L. alpenae* and *L. johannae* of Lakes Michigan and Huron, but positive identification was difficult because so few specimens were available. A tentative identification as *L. johannae* (Scott, 1954) was, however, made because gill-raker counts of the few fish taken matched *L. johannae* better than *L. alpenae*.

A general fishery survey of Lake Erie by the United States Bureau of Commercial Fisheries in 1957 again turned up a couspicuously different cisco in the east end of the lake. Biologists of the research vessel *Cisco*, unaware of the specimens taken in 1946 and 1947, tentatively identified their first specimens as *L. alpenae* because of the close resemblance to the same species of Lake Huron where they had conducted a fishery survey in 1956. By the end of the year 26 specimens had been collected, 16 from one gill-net set on November 13, 1957. Further examination of the 33 specimens collected in 1946–47 and 1957 now permits their positive identification as *L. alpenae*.

MATERIALS AND METHODS

Six longjaw ciscoes used in this study were taken in August and September 1946 from commercial gill nets fished near Port Dover, Ontario (ROM Nos. 13728, 13729, 13733, 13757, 13759). Another specimen was obtained from a commercial catch landed at Erieau, Ontario, in July 1947 (ROM No. 13755).

Twenty-six specimens were collected in May–November 1957 in the vicinity of Long Point in eastern Lake Erie (UMMZ Nos. 178,808–178,816, ROM No. 21,808). Of these, 24 were taken in experimental gill nets fished by the research vessel *Cisco* (United States Bureau of Commercial Fisheries) on the bottom at 33–34 fathoms (60–62 m). One specimen was caught in a trawl dragged on the bottom in 17 fathoms (31 m) and another was taken within 20 feet (6 m) of the bottom in a gill net fished from the surface to the bottom at 80 feet (24 m).

Morphometric measurements and counts generally folllow those used by Koelz except that dorsal and anal ray counts include all rays regardless of length; this procedure increased counts by 1 or 2 (averages, 1.8 and 1.4, respectively) over those of Koelz (1929). Measurements and counts in addition to those made by Koelz include: the distance from the tip of the snout (junction of premaxillaries) to the insertions of the pectoral and ventral fins; the interorbital distance—least distance across the top of the head between bony margins of the orbits; length of lower gill arch—distance from lateral insertion of center gill raker to the anterior base of the anterior gill raker on lower arm of the first gill arch; length of center gill raker—distance from lateral insertion of the center gill raker to its tip; the number of scale rows around the body immediately anterior to the dorsal fin; and number of scale rows around the caudal peduncle immediately anterior to the dorsal insertion of the caudal fin.

All counts and measurements were made on the 26 specimens collected in 1957. Several counts and measurements were made of the 7 specimens collected in 1946–47 shortly after collection. As these fish were measured fresh and the 26 specimens collected in 1957 were measured after 2 years of preservation, discussions of measurements are based mainly on the later collections to avoid discrepancies that may have resulted from shrinkage following preservation. A summary of measurements and counts for the 26 fish collected in 1957 is given in Table I.

Comparisons are made with data presented by Koelz (1929), and with 25 *L. alpenae* and 26 *L. artedi* collected in Lake Huron in 1956. The 13 *L. artedi* collected along with *L. alpenae* in Lake Erie in 1957 are used to show distinguishing characteristics between the species. Proportions based on body measurements were used for only 11 *L. artedi* as 2 had badly deformed vertebral columns and distorted bodies.

The authors are indebted to Mr LaRue Wells who collected specimens used for this study during the cruises of the research vessel *Cisco* in 1957.

IDENTIFICATION

Koelz (1929) found *Leucichthys alpenae* to resemble *Leucichthys johannae* more closely than any other cisco of the Great Lakes. The most discriminating means of distinguishing between the two species were differences in numbers of gill rakers, lateral line scales and pectoral rays, and in the pectoral-ventral distance/pectoral length (PV/P) and ventral-anal distance/ventral length (VA/V) ratios. Koelz's comparisons between the two species in Lakes Michigan and Huron showed that *L. alpenae* tended to have a greater number of gill rakers,

TABLE I. Proportional measurements of *L. alpenae* collected in Lake Erie, expressed in thousands of standard length.

Measurement	Mean	Range
Body[1]		
Standard length (millimeters)	245	219–268
Snout to adipose origin	853	836–878
Snout to dorsal origin	506	487–526
Snout to anal origin	784	761–813
Snout to ventral insertion	549	517–579
Snout to pectoral insertion	228	211–242
Pectoral insertion to ventral insertion	330	297–358
Ventral insertion to anal origin	253	234–287
Body depth	241	218–276
Body width	142	121–201
Caudal peduncle depth	75	68– 83
Fins[1]		
Pectoral length	171	160–184
Ventral length	172	148–184
Anal height	119	108–134
Anal base length	107	94–148
Dorsal height	170	100–187
Dorsal base length	107	90–128
Adipose length	75	67– 84
Head[1]		
Head length	233	220–248
Head depth	150	144–162
Mandible length	115	101–123
Maxillary length	86	76– 99
Snout length	62	57– 67
Eye diameter	52	48– 57
Interorbital distance	64	54– 73
Lower gill-arch length	107	100–113
Center gill-raker length	36	31– 42
Counts[2]		
Gill rakers	36	30– 39
Lateral line scales	76	68– 83
Scale rows around body	41	38– 45
Scale rows around caudal peduncle	20	18– 21
Vertebrae	58	56– 59
Dorsal fin rays	12	10– 13
Anal fin rays	12	10– 14
Pectoral fin rays	15	13– 16
Pelvic fin rays	11	10– 13

[1]Measurements of 26 fish collected in 1957.
[2]Counts of 7 fish collected in 1946–47 and 26 fish collected in 1957 except for scale rows and pectoral rays which include only the latter.

fewer lateral line scales, fewer pectoral rays, and larger PV/P and VA/V ratios than *L. johannae* (Table II). Koelz's series of collections of ripe and spent *L. johannae* indicated a spawning period from late August into September, but he had only indirect evidence that *L. alpenae* spawned in November, a period later confirmed by Jobes (1949). Although the counts and measurements showing differences between the species may overlap, the different spawning periods demonstrate reproductive isolation.

Counts and ratios of the *L. alpenae* taken in Lake Erie in 1946–47 and 1957 agree very closely with the records of Koelz for this species in Lake Huron and Michigan, and show the same differences used by Koelz in distinguishing them

TABLE II. Counts and measurements that distinguish *L. johannae* and *L. alpenae* in lakes where they occur. Figures in parentheses are extremes of range, and central figures give 80–90% range. Data from Lakes Michigan and Huron are from Koelz (1929).

Species and lake	Gill rakers	Lateral line scales	Pectoral-ventral /ventral	Ventral-anal /ventral	Pectoral rays
Leucichthys johannae					
Lake Michigan	(26)27–32(36)	(74)80–90(95)	(1.5)1.6–1.8(2.1)	(1.1)1.2–1.5(1.6)	(14)16–17(20)
Lake Huron	(25)27–31(35)	(67)77–87(91)	(1.3)1.5–1.8(2.1)	(1.0)1.2–1.4(1.6)	(15)17–18(19)
Leucichthys alpenae					
Lake Michigan	(33)36–43(46)	(71)78–85(96)	(1.6)1.9–2.2(2.5)	(1.2)1.4–1.7(1.9)	(12)15–17(18)
Lake Huron	(31)34–40(44)	(70)76–83(91)	(1.6)1.8–2.1(2.3)	(1.3)1.4–1.7(1.9)	(14)15-17(18)
Lake Erie	(30)31–38(39)	(68)72–81(83)	(1.7)1.8–2.1(2.2)	(1.3)1.4–1.7(1.8)	(13)14–16

from *L. johannae* (Table II). Although gill-raker counts of *L. alpenae* in Lake Erie are lower than in Lakes Huron and Michigan, approaching the counts of *L. johannae*, the number of lateral line scales and pectoral rays for *L. alpenae* in Lake Erie are more divergent from *L. johannae* than in the other lakes. The PV/P and VA/V ratios of *L. alpenae* show the same degree of difference from *L. johannae* in all three lakes. All of the *L. alpenae* taken in Lake Erie on November 11, 1957, were ripe and had well developed pearl organs. The indication of a late-November spawning period is in agreement with the spawning period of this species in other lakes and differs from the August–September spawning of *L. johannae*.

The possibility of confusing *L. alpenae* with *L. johannae* has been much reduced if not eliminated in recent years. In 1954–55 no *L. johannae* were found in a study of the chubs of Lake Michigan (Moffett, 1957) and none were found during a similar study of southern Lake Huron in 1956. These observations may indicate that the species has become either extremely rare or extinct. Its moderately large size and deepwater habitat would have made it particularly vulnerable to depredation by the sea lamprey during and particularly following destruction of the lake trout in these lakes (Hile, 1949; Hile *et al.*, 1951; Eschmeyer, 1957).

Clemens (1922) described 5 separate species of ciscoes in Lake Erie. Koelz (1929) later included 4 of these species in a list of synonyms for *L. artedi*, and believed that the fifth, *L. prognathus*, was actually *L. artedi albus* based upon his own examination of ciscoes from the eastern end of Lake Erie. Koelz (1924) considered *L. prognathus* conspecific with *L. alpenae*, but also gives it in synonym lists for *L. hoyi* and *L. nigripinnis* (Koelz, 1929). The present record of *L. alpenae* in Lake Erie again raises the question of the status of *L. prognathus* reported by Clemens which he called the longjaw cisco. Clemens reported that his longjaw cisco was taken in eastern Lake Erie between Port Dover and Port Maitland which is within the area inhabited by *L. alpenae* of the present report. Clemens also described his longjaw cisco as having a ". . . long mandible which usually extends beyond the upper jaw . . . relatively long bony snout . . . narrow caudal peduncle . . . ", which are all characteristic of our *L. alpenae*. The

gill-raker counts, however, ranged from 41 to 46 and fall well outside the range of *L. alpenae* and within the range of the Lake Erie lake herring. Thus the longjaw described by Clemens could not have been the same as the longjaw reported here, and must have been no more than a selected group with similar features from the highly variable population of *L. artedi*, as were the other 4 species described by Clemens.

The only other record from Lake Erie that may have a bearing on our record is based on a single specimen taken from fish landed at Erie, Pennsylvania, in December 1914 that were caught in the deep hole north of Erie. This specimen (U.S. National Museum No. 76,845) was described by Bean (1916) as a new species, *L. macropterus*. This specimen was characterized by very long pectoral, pelvic, dorsal and anal fins which were 39, 44, 35, and 29 percent of the body length respectively. This fish has been considered an anomalous specimen by subsequent authors (Dymond, 1922; Koelz, 1929) and ignored since no specimens like it have subsequently been taken. The body proportions given by Bean agree reasonably well with those of our *L. alpenae*, and the gill-raker count of 30 gives good reason to believe that this specimen may have been an aberrant *L. alpenae* rather than *L. artedi* as believed by other authors.

DISTINGUISHING CHARACTERS

The longjaw cisco is one of 3 coregonid species inhabiting Lake Erie. The other 2 are the lake herring and the lake whitefish (*Coregonus clupeaformis*). The whitefish is very clearly distinguishable from the ciscoes of the Great Lakes by its retrorse premaxillaries, subterminal mouth, and low gill-raker number.

In gross appearance the longjaw cisco stands apart from the lake herring because of its heavier and larger head and head parts, a blunter nose (as viewed from above), and generally lighter pigmentation, particularly of the mouth parts. The tip of the lower jaw also tends to extend beyond the premaxillaries in nearly 50% of the specimens whereas the jaws of lake herring are usually equal. The common name "longjaw cisco" was given to populations from Lakes Michigan and Huron where the lower jaw extends beyond the upper in nearly every specimen.

Although the dimensions of the head and head parts are useful in distinguishing between the longjaw cisco and lake herring, proportional measurements of these do not provide as satisfactory a separation of these species in Lake Erie as in Lake Huron. The relative length and depth of the head is clearly greater for *L. alpenae* in both Lakes Huron and Erie but the distributions of ratios overlap much more broadly in Lake Erie than in Lake Huron (Table III). A similar comparison of mouth size is demonstrated by the frequency distributions of maxillary and mandible lengths (Table IV). Other head parts show similar relations. Measurements of head size and mouth size provide an almost complete separation of the species in Lake Huron, but are of limited value in Lake Erie where identification must be based largely on gross appearance. Thus in field identification of fish from Lake Erie, those fish for which several or all of the head

TABLE III. Frequency distribution of head length and head depth divided by standard length of *L. alpenae* (*alp*) and *L. artedi* (*art*) in Lakes Erie and Huron.

Head length/standard length					Head depth/standard length				
Thousandths of standard length	Lake Erie		Lake Huron		Thousandths of standard length	Lake Erie		Lake Huron	
	alp	*art*	*alp*	*art*		*alp*	*art*	*alp*	*art*
205–209	...	...	...	1	120–124	...	...	...	1
210–214	...	2	...	3	125–129	...	...	...	8
215–219	...	2	...	6	130–134	...	1	...	7
220–224	2	1	...	7	135–139	...	1	3	8
225–229	6	2	1	2	140–144	3	2	2	1
230–234	6	2	3	2	145–149	9	3	6	1
235–239	8	2	3	3	150–154	11	4	4	...
240–244	3	...	1	2	155–159	2	...	5	...
245–249	1	...	5	...	160–164	1	...	3	...
250–254	...	...	2	...	165–169	...	...	1	...
255–259	...	...	5	...	170–174	...	...	1	...
260–264	...	...	3	...					
265–269	...	...	2	...					
Number of fish	26	11	25	26		26	11	25	26
Average	233	227	249	224		150	146	151	132

TABLE IV. Frequency distribution of the maxillary and mandible lengths divided by the standard length of *L. alpenae* (*alp*) and *L. artedi* (*art*) in Lakes Erie and Huron.

Maxillary length/standard length					Mandible length/standard length				
Thousandths of standard length	Lake Erie		Lake Huron		Thousandths of standard length	Lake Erie		Lake Huron	
	alp	*art*	*alp*	*art*		*alp*	*art*	*alp*	*art*
55– 59	...	...	...	1	90– 94	...	...	...	3
65– 69	...	...	...	2	95– 99	...	2	...	4
70– 74	...	1	...	6	100–104	1	1	...	7
75– 79	2	4	...	11	105–109	5	3	...	7
80– 84	7	5	...	2	110–114	5	3	1	3
85– 89	11	1	2	1	115–119	9	2	4	2
90– 94	4	...	6	3	120–124	6	...	5	...
95– 99	2	...	7	...	125–129	...	...	7	...
100–104	...	...	8	...	130–134	...	...	3	...
105–109	...	...	1	...	135–139	...	...	4	...
110–114	...	...	1	...	140–144	...	...	1	...
Number of fish	26	11	25	26		26	11	25	26
Average	86	79	98	77		115	108	127	104

features tend to be heavier would be classed as *L. alpenae*. Of course other features such as degree of pigmentation, bluntness of snout, and protruding lower jaw are considered.

With experience, fish can be identified by these characters with a high degree of accuracy, but head features are not good taxonomic characters as they can be modified by the environment (Hile, 1937; Svärdson, 1950, 1951). Indeed, environmental influences may be largely responsible for greater similarity between the longjaw cisco and lake herring in Lake Erie than in Lake Huron. Both species are found together below the thermocline in the restricted area of the

deeper (maximum depth 35 fathoms or 64 m) eastern basin of Lake Erie during most of the year. Recent evidence of summer oxygen depletion (Carr, in press) and temperature increase Beeton (1961) in other areas of the lake suggest even greater confinement to the limited cold-water segment of the lake. In Lake Huron, however, lake herring are distributed throughout shallower areas of the open lake while the longjaw cisco inhabits the extensive deeper areas. Thus, if environment did influence head proportions, one would expect greater similarity in Lake Erie than Lake Huron, almost to the limit of the genotypic plasticity of the two species.

More positive distinction can be made between the longjaw cisco and lake herring of Lake Erie by gill-raker counts (Table V). This character has been demonstrated in transplantation experiments of coregonids to be little influenced by the environment. In fact, gill-raker counts of the two species are better separated in Lake Erie where the species live in a more restricted environment than in Lake Huron where they occupy different habitats (Table V). This situation is the reverse of the relationship of head features. Although collections of *L. alpenae* taken in 1946–47 and 1957 showed no overlap in gill-raker counts with *L. artedi* collected in 1957 or the range of 41–53 reported by Koelz (1929) for Lake Erie, counts of over 1300 *L. artedi* collected in 1946–47 ranged from 37 to 53 (Scott 1950), indicating some overlap.

TABLE V. Frequency distribution of gill-raker counts of *L. alpenae* and *L. artedi* in Lakes Erie and Huron.

Number of gill rakers	Lake Erie		Lake Huron[3]	
	alpenae[1]	*artedi*[2]	*alpenae*	*artedi*
30	2	...	...	...
31	1	...	...	...
32	1	...	...	...
33	4	...	1	...
34	5	...	1	...
35	7	...	3	...
36	5	...	5	...
37	5	...	4	...
38	2	...	5	...
39	1	...	3	...
40	...	...	1	...
41	...	...	1	2
42	...	2	1	...
43	...	1	...	2
44	...	1	...	2
45	...	2	...	2
46	...	3	...	7
47	...	1	...	2
48	...	...	...	6
49	...	1	...	1
50	...	2	...	1
51	...	...	...	1
Number of fish	33	13	25	26
Average	34.8	45.8	37.2	46.2

[1]1946–47 and 1957 collections.
[2]1957 collections.
[3]1956 collections.

A simple discrimination index based on gill-raker number, gill-raker length, and length of the lower arm of the gill arch has been used successfully to distinguish among several species of European coregonids (Dottrens, 1959). The lengths of the lower gill arch and the center gill raker are of considerable value in separating *L. artedi* and *L. alpenae* of Lake Erie although some overlap occurs (Table VI). The formula below yields a broad separation of *L. alpenae* and *L. artedi* in Lake Erie:

$$F = R + \left(\frac{100\ CR}{LA}\right)$$

Where: F = a discriminant function
R = number of gill rakers
CR = length of center gill raker
LA = length of lower gill arch

Values of F for individual *L. alpenae* ranged from 64 to 77 (mean 69.2) and for *L. artedi* from 82 to 96 (mean 89.5). These values, in a sense, provide a numerical expression of the discrimination used in distinguishing between species by gross examination where the relationships among several characteristics are considered simultaneously.

TABLE VI. Frequency distribution of the lower gill-arch and center gill-raker lengths divided by standard length of *L. alpenae* (*alp*) and *L. artedi* (*art*) of Lake Erie.

Length of lower gill arch/standard length			Length of center gill raker/standard length		
Thousandths of standard length	*alp*	*art*	Thousandths of standard length	*alp*	*art*
84– 85	...	1	31	1	...
86– 87	...	2	32	1	...
88– 89	...	1	33	4	...
92– 93	...	1	34	2	...
94– 95	...	1	35	1	1
96– 97	...	2	36	7	1
98– 99	...	1	37	5	...
100–101	2	1	38	2	...
102–103	5	...	39	...	...
104–105	4	1	40	2	3
106–107	3	...	41	...	2
108–109	5	...	42	1	1
110–111	5	...	43	...	3
112–113	2	...	...	...	...
Number of fish	26	11		26	11
Average	107	94		36	40

AGE, GROWTH AND MATURITY

The 6 longjaw ciscoes collected in 1946 belonged to age-group III (3 completed annuli), and the single specimen of 1947 to age-group IV, thus all were members of the 1943 year-class. Of the fish collected in 1957 all but one belonged to age-group III and the remaining specimen, the first collected that year (in

May) belonged to age-group IV. Sampling in 1956 was by graded gill nets of 1- to 4-inch mesh with longjaw ciscoes taken in 1½- to 3-inch mesh. Hence, either few fish live beyond age III, or else the two sampling periods by chance coincided with periods when two dominant year-classes had reached age III.

Total length of the 6 longjaw ciscoes taken in 1946 at age III ranged from 12.2 to 13.6 inches and averaged 12.8 inches (310–345 mm, av. 325) and the age-group IV fish taken in 1947 was 13.7 inches (348 mm).[3] The 25 age-group III fish taken in 1957 ranged from 10.2 to 12.6 inches and averaged 11.6 inches (259–320 mm, av. 295 mm) and the single age IV fish was 11.7 inches (297 mm) long. The decrease of 1.2 inches (30 mm) for III-group fish between the 1946 and 1957 collections reflects poorer growth and may, in part, have been influenced by recent indications of progressive eutrophication of Lake Erie (Beeton, 1961).

The growth rate as determined by back calculation from scale measurements of longjaw ciscoes collected in 1957 follows the classical growth pattern (Table VII). This growth rate compares favorably with calculated total lengths of 5.6, 8.3 and 10.3 inches (142, 211, 262 mm) at the ends of years 1, 2 and 3 respectively, reported by Jobes (1949) for the longjaw of age-group III, from Lake Michigan. Both the growth pattern and growth rate are, however, in sharp contrast with that of the lake herring taken in the same nets with the longjaw ciscoes in Lake Erie (Table VII). The lake herring averaged only 2.7

TABLE VII. Comparison of the growth of *L. alpenae* and *L. artedi* of age-group III collected in the same nets in Lake Erie in 1957. Lengths shown are total lengths calculated from scale measurements.

Species	No. of fish	Length at end of year of life			Length at end of year of life		
		1	2	3	1	2	3
		inches	*inches*	*inches*	*mm*	*mm*	*mm*
L. alpenae	25	5.1	8.6	10.6	130	218	269
L. artedi	10	2.7	7.6	10.3	69	193	262

inches in their first year—nearly half the 5.1 inches of the longjaw cisco.[4] Much more rapid growth of the lake herring during the next two years narrowed the gap between the species to 0.3 inches. It is most unusual, however, to find a fish that hatches in the early spring to grow less in its first year than in its second—certainly a phenomenon not known in any other coregonid population. The resultant scale pattern in *L. artedi* was so strinkingly different from *L. alpenae* it served as an additional distinguishing characteristic separating the longjaw ciscoes and lake herring collected in 1957.

All specimens of longjaw ciscoes taken in Lake Erie in 1957 were mature indicating that maturity must be reached at least by the start of the fourth

[3]Total lengths (to the longer tip of the tail when adjusted to the position of maximum extension) were calculated by multiplying standard length, measured when fish were fresh, by 1.1986; this factor was obtained from measurements of specimens collected in 1957.

[4]Cursory examination of lake herring scales collected in the 1940's showed a normal growth pattern with rapid growth in the first year.

growing season. Specimens taken on November 13 all had very well developed gonads, and one male appeared to be at least partly spent. The lake herring taken early in November also had well developed gonads, but appeared to be a little farther from spawning. Pearl organs of the lake herring were also not as well developed as those of longjaw ciscoes taken at the same time.

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Some Considerations in the Study of Respiratory Metabolism in Fish, Particularly Salmon[1,2]

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ABSTRACT

A general review of the basis and measurement of respiratory metabolism in fish is presented, with particular reference to sources and magnitudes of influence (error) which various major factors can impose. There is a continuing need for precise measures of metabolism, including quantitative estimates of excretory products, both intrinsically and as a basis for assessing the effect of environmental change. The metabolic cost of locomotion at all levels of performance requires exact definition. Efficiency of performance for fish cannot be determined without a suitable means of relating energy expended to work performed. It is suggested that comparisons be made on the basis of energy required for a propulsion rate of 1 body length per second.

INTRODUCTION

During the last ten years the stocks of Pacific salmon (genus: *Oncorhynchus*) which migrate through many of the major and minor rivers in British Columbia, Canada, have been subjected to the effects of gradual if not rapid industrial expansion, particularly from hydroelectric and pulpmill developments. A great deal of information on the physiology and behaviour of salmon is necessary if only to assess possible damage, let alone provide solutions.

One of the recurring questions has been that of the amount of energy which a salmon requires in order to meet the demands of migration, maturation and spawning. There is the possibility that environmental changes would so alter these processes that available metabolic fuels would be exhausted prior to effective spawning. The procession in the depletion of fat and protein which accompanies the migration of certain races of adult sockeye (*O. nerka*) in the Fraser River has been worked out in considerable detail by Idler and Clemens (1959). Over 90% of the body fats may be utilized and, in the female, 50 to 60% of the total protein. These analyses provide the factual circumstance under *existing* environmental conditions. Except for the fraction of body constituents which is mobilized in the developing gonads, it is quite understandable that it is impossible to say what such separate functions as maintenance and swimming require in the way of energy, and to predict the consequences of elevated temperature as a source of energy drain. Conveniently, the termination of feeding which characterizes freshwater entry and upstream movement of salmon eliminates the problem of assessing the accrued energy from ingested food.

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In another vein, the effects of dilute toxic constituents on the activity of young and adult salmon have been questioned. The assessment of sub-lethal concentrations is handicapped by lack of suitable criteria. Since in many instances the environment acts through metabolism on activity (Fry, 1947) the need for highly accurate measures of metabolism under particular conditions has arisen, together with the need for a detailed description of the normal metabolic relations in the five species of Pacific salmon which inhabit the eastern Pacific.

The following review of the general concepts and an examination of the potential sources of error in dealing with the respiratory metabolism of fish was made to provide a background for the research contemplated.

BASIC CONSIDERATIONS

Davson (1951) gives a good discussion of the basic phenomena of metabolism, and Brody (1945) deals with energy exchange in domestic animals. Fry's 1957 account of metabolism provides a source for surveying much of the present status of knowledge for fish, while Black's (1958a) discussion of energy stores and metabolism gives a penetrating account of the problem in relation to biochemical exchange (see also Black *et al.*, 1961). Recent translation of Winberg's (1956) monograph brings to light not only an excellent review but also a segment of research on fish metabolism which has not been readily available previously.

In general, if an animal does not alter its potential energy status during a given period, the energy made available by metabolism is equal to the heat produced (first law of thermodynamics).

According to the second law of thermodynamics, "the liberation of heat is a necessary accompaniment of any transformation of energy of whatever sort, even when carried out at maximum efficiency, so that all the varied transformations of energy accompanying metabolism are also accompanied by the liberation of heat. The more inefficiently these processes are carried out, in a thermodynamic sense, the more heat appears as a by-product" (Davson, 1951). Contraction of the skeletal muscle is one of the most efficient processes in higher organisms, yet even here some 80% of the liberated chemical energy appears as heat.

Metabolism may be measured therefore by direct calorimetry in which the amount of heat liberated is determined. This is not a particularly appropriate technique for fish, mainly because of the problem of measuring heat liberation in water with its large specific heat and consequent insensitivity to temperature change, and the relatively low metabolic rate of poikilotherms.

The unspecified metabolic demand in migrating salmon has been determined in the case cited earlier (Idler and Clemens, 1959) and in previous studies (Pentegov *et al.*, 1928) by performing proximate analyses on samples taken at various points in the upstream passage. The calorific value of the average loss of body fuels was not directly determined, standard equivalents from mammalian studies being applied.

Rubner (cited by Brody, 1945) in a classical experiment using a respiration calorimeter, showed that the calculated heat production from the chemical

exchanges equalled the actual heat production within 1%, introducing the method of indirect calorimetry. As oxygen is the only element in aerobic animals used in respiration, any measure of oxygen uptake can be used as a measure of metabolism, provided oxygen debt is not involved. However, this is not an *exact* measure of the energy made available to the animal since different constituents may be oxidized and the extent and proportion of these determines the energy equivalents. To assess the expended energy, the relative utilization of carbohydrate, fat or protein must be known, and their calorific equivalents[3]. This may be obtained by use of the well-known Respiratory Quotient or R.Q. (ratio of CO_2 to O_2) which has a value of 1.0 for carbohydrate, 0.72 for fat, and 0.80 for protein. Since the three processes may be simultaneous, the amount of protein is estimated from the amount of nitrogenous waste excreted. Among such teleosts as have been studied critically, a large proportion of their nitrogen is excreted as ammonia and urea from the gills, most of the balance appearing as creatine, creatinine, amino acid and uric acid in the urine (V. S. Black, 1957; Wood, 1958). Kleerekoper and Mogensen (1959), in studying the scent of certain freshwater fish, have added to the number of identifiable nitrogenous constituents excreted and possibly secreted. These include 9 amino acids and 10 amines. Ammonia constituted 98% of the total amino nitrogen.

As has been frequently pointed out, fat is the advantageous storage fuel since for unit weight it provides over twice the energy of carbohydrate or protein. Being greatly reduced, it requires a lot more oxygen to convert fat to H_2O and CO_2. If the metabolic oxycalorific equivalents for unit uptake of oxygen are considered, the differences are considerably reduced, viz., carbohydrate 5.05, fat 4.74, and protein 4.46 (Cal per litre of O_2, determined in mammals). Since the inevitable large by-product of heat is of no value to the aquatic poikilotherm it can "afford" to get by on a very low standard metabolism. It should also be noted that the above equivalents may not be entirely representative of the metabolic fuels and oxidative pathways in fish. If we accept the above and consider the extreme possibility of a fish which had recently fed and was obtaining energy from carbohydrate and compare this with a starved fish of similar dimensions forced to derive its energy from protein, the latter would require 10% more oxygen. If it can be shown that the *proportion* of gases liberated (O_2, CO_2 and NH_3) remains relatively constant, then a measure of the changes in oxygen uptake accompanying different levels of metabolism can be taken as a direct reflection of the energy changes accompanying these activities.

TERMINOLOGY

The actual energy available for work of all sorts (osmotic, mechanical, structural change, overcoming friction, etc.) is called the *free energy* of the chemical reaction. The total amount of energy set free (including heat) is the

[3]The heat of combustion of glucose is 3.7 Cal/g (kilo-calories per gram); the equivalent for a typical fat 9.3 Cal/g, and that for protein 4.1 Cal/g (Brody, 1945). These values vary somewhat according to the particular organic compounds considered and whether the physiologic equivalent, which takes into account the energy level of excretory products, is determined.

heat of reaction. According to Hess' Law, this is true whether the reaction proceeds in one step or by a multitude of stages, so long as the end-products are the same (Davson, 1951).

Both *basal* and *resting* metabolism have been used to denote the minimum metabolic rate accompanying the energy cost of maintenance. This cost relates to the minimum functions of circulation, respiration, excretion and muscle tone which never cease, even under absolute rest. It also constitutes the energy wastes associated with activities of enzyme systems, colloidal structures, semi-permeable membranes and the maintenance of protoplasm. It does not relate to the energy expended for growth or morphogenesis, the transformation of food intake, or the internal transforming of simple precursors into more complex states. These constitute the energy of *morphogenetic work* (Brody, 1945).

In practice, basal metabolism is defined as the minimum energy cost when the animal is at rest in a thermoneutral (or temperature acclimated) environment in the post-absorptive condition. The possibility of obtaining absolute rest has frequently been questioned for undomesticated animals or animals subject to excitement from handling or experimental confinement. This has led to the use of *standard metabolism*, which is employed in relation to fish metabolism and is taken to be the least rate of metabolism commensurate with appropriate experimental techniques. It is usually measured after 24 hours of fasting, during the slump of any diurnal metabolic cycle.

Active metabolism is the maximum rate consistent with the highest continued level of activity. It has a characteristic level for any temperature. Here again there has been some problem of absolute determination since different investigators have used different methods of stimulation and the question of maximum activity is left in some doubt (e.g., Basu, 1959).

Routine metabolism has been used to express the average oxygen consumption of fish which are moderately active (e.g., Job, 1959; Wohlschlag, 1960) or which are undergoging continuous oxygen recording during "free" activity in a sealed aquarium. It forms a closer approximation of normal demand since no animal is continuously resting or maintaining peak activity. Some justification for its use relates to the fact that a good many determinations of active metabolism in fish have not exceeded the standard levels by more than 3 to 4 times (Fry, 1957) so that routine rates are likely to approximate an average metabolic demand and, lacking better evidence, be useful in estimates of energy requirements in food turnover.

OXYGEN DEBT

During prolonged hard work, mammals may expend from 10 to 15 times the energy at rest, whereas during very intense muscular work, which cannot be prolonged because of rapidly onsetting fatigue, they may expend over 20 times the basal rate, using anaerobic energy reserves. The animal goes into *oxygen debt*. This is associated with an increase in the products of anaerobic oxidation such as pyruvic acid and lactic acid as well as a decrease in concentration of phosphocreatine and adenosine triphosphate (ATP). The recovery

phase at rest is associated with the reverse process, characterized by continued deep respiration.

The importance of eliminating the involvement of oxygen debt in any metabolic measures which relate activity to oxygen consumption can hardly be overemphasized. If unknown debt is being incurred, it means that the rate of uptake is less than the demand and consequently an error would be introduced if performance were being related to consumption. As has been recognized, active metabolism as defined is not so much a characteristic of the particular cellular demand, but of the primary circumstances of oxygen extraction, transport and delivery to the respiring tissues.

If resting metabolism is being determined, a serious error can be introduced if the oxygen debt from earlier excitation is not fully replaced. Although physically resting, respiration will be elevated. Post-ventilation in man following strenuous exercise can persist for 20 or 30 minutes. The relation in fish is not known. Considering the comparatively prolonged period of elevated blood lactate, amounting to 6–8 hours, which Black and associates (1958b, 1960) have reported for some salmonids following exhaustive exercise, similarly long periods may be required for complete oxygen debt replacement.

Blazka (1958) has studied the increased oxygen consumption in trout (*Salmo trutta*) following a period of debt imposed by temporarily reducing the oxygen below the critical level necessary for resting metabolism. Greatly increased uptake characterized the post-hypoxic period with replacement occurring in about 1½ hours. No such replacement was reported for the carp by this author, who contends that this species must form harmless, stored end-products of anaerobic metabolism, at least when not exposed to exercise. Reduction of oxygen debt following fatigue in "trained" and "untrained" rainbow trout (*Salmo gairdneri*) at 4°C has recently been reported to require 5 to 6 hours, with the trained group able to sustain a 50% greater debt (Hochachka, 1961). Debt from deprivation of oxygen and that from fatigue may involve different metabolic paths and rates of replacement. Temperature level is apparently important.

FACTORS AFFECTING METABOLISM

The student of metabolism has many hazards to contend with in obtaining accurate, reproducible measures of metabolism, among which oxygen debt is merely one. The variability within the data presented by authors is frequently large, and a comparison between authors for the same species shows differences which at times defy reasonable interpretation (cf. Winberg, 1956). The question hinges on the error due to variability inherent within the species and the error imposed by insufficient attention to adequate control or assessment of variables preceding and during experimentation. Many of the environmental factors involved have been considered by Fry (1957). A brief examination of these with a view to pointing out the magnitude of potential error is revealing.

Activity. As noted, activity has a tremendous effect on metabolism, frequently elevating the oxygen uptake by a factor of 4 times at optimum tem-

peratures and reaching a maximum of 8 times in one species to judge from data presented by Winberg (1956) for chum salmon (*O. keta*). Activity should always be recorded by one means or another. Spoor's (1941, 1946) earlier work and that reported by Fry (1957) lend emphasis to this requirement. It can easily be seen that either through undocumented or unsuspected presence of activity (e.g., elevated muscle tone) the error from this source could be very large indeed when determining standard metabolism. In the case of active metabolism, undernourished, unexercised, disease-inhibited, sluggish or lazy fish could reduce the potential level. However, excitation and oxygen debt replacement (unless depressed by excessive waste products) make large demands on metabolism and hence do not detract from determining this latter index. Since ventilation of the gill chamber could be the limiting factor, and free swimming rather than just free opercular movement can facilitate ventilation, the circumstances within the respirometer must not be overlooked.

Oxygen. The gill system of fish is remarkably efficient, working on the counter-current principle and capable of removing 80% of the oxygen from the respired water (Van Dam, 1938). When there is excess oxygen (respiratory independence) no limitation to activity is imposed. Below this level of excess, active metabolism is dependent on oxygen availability (respiratory dependence). Where standard metabolism becomes dependent, any continued activity will result in death from irreplaceable oxygen debt (level of no excess activity — Fry, 1947).

The consequent potential error of insufficient oxygen supply expresses itself usually in affecting determinations of active metabolism. For instance, Katz *et al.* (1959) found that juvenile chinook salmon (*O. tshawytscha*) required a 50% higher level of oxygen (3.0 mg/l) when swimming for 24 hours at 0.8 ft/sec (24 cm/sec) than that for a resting state (2.0 mg/l). The presence of sufficient oxygen must therefore be established. Air saturation may not always achieve this state of excess as appears to be the case for the speckled trout, *Salvelinus fontinalis* (Job, 1955).

Carbon dioxide. Oxygen availability can be reduced by the interference of CO_2, NH_3 and altered pH as a consequence of excretion. Basu (1959) has performed one of the most thorough studies on four species of fish relating levels of CO_2 and O_2 to active metabolism. Contrary to the impression gained in earlier literature, Basu reports that the active metabolic rate diminishes exponentially with *any* increase in carbon dioxide. This finding is undoubtedly due to the unusually high level of activity which was maintained in his respirometer. Winberg (1956) had previously concluded that only at considerable elevation would any depressing effect from CO_2 be present. This is apparently only true for inactive states. Since the amount of CO_2 dissolved in normal waters is low (2 ppm) it would take a tenfold increase to depress the most active rate of oxygen consumption in speckled trout by 20%.

Ammonia. Comparatively little is known about the rate of production of excreted ammonia. From preliminary experiments in our laboratory and a compilation by Saeki (1957) it appears to range from at least 2 to 20 mg/kg/hr.

Kleerekoper and Mogensen (1959) report an intermediate level of approximately 10 mg/kg/hr for brook trout. In waters near the neutral point ammonia exists mainly in the ionized non-toxic state (dissociation ratio = 180:1 at 25°C). Un-ionized ammonia can be toxic at a concentration as low as 0.3 parts per million (Anon., 1952). With CO_2 present there is also ionization of ammonium carbonate. Thus, *unless* a significant rise in pH occurs, ammonia will be mainly in the non-toxic state so that no great concern need be felt. Lloyd and Herbert (1960) have shown that in an alkaline medium the effect of expired CO_2 at the gill surface is to decrease the toxicity of ammonia by shifting the pH toward the neutral point. Additional research on the nature, rates and factors affecting nitrogenous metabolism in fish is sorely needed.

HYDROGEN-ION. Fish are known to inhabit waters of a wide variety of pH, ranging from 5.0 to 9.0 (Doudoroff and Katz, 1950). Despite this wide range to which fish have shown a capacity to adapt, rapid changes in pH can accelerate oxygen consumption at least temporarily (Wiebe *et al.*, 1934). Examination of the related factors causing change in hydrogen-ion concentration is paramount since the radicals involved may well be toxic. A change in pH can consequently introduce unidentified error. A constancy of at least $\pm$ 0.5 should be maintained within the respirometer. Job (1955) points out that this is equivalent to about $\pm$ 12 ppm CO_2 at an alkalinity of 200 ppm as carbonate.

TEMPERATURE. The level of both active and standard metabolism can be altered 5- to 10-fold by a temperature change of 20°C in the presence of excess oxygen. The magnitude of change for unit change of temperature tends to be greater in the lower range of temperature (5 to 10°C) in the case of active metabolism (for fish which show a metabolic dependence on the availability of oxygen at high temperatures, e.g., most salmonids). Standard rates, however, show greatest change at elevated temperatures. It is quite conceivable that an error of 20% could occur by an unrecorded elevation of 1°C. The lack of either adequate recording or precise control could introduce disturbing differences.

Krogh's (1914) empirical curve relating temperature and resting metabolism in a wide variety of animals is shown by Winberg (1956) to have quite a universal though not always exact application among different species of fish. As Winberg observes, it is unfortunate that the relation cannot be expressed by some direct equation. When plotted as the logarithm of consumption against temperature, moderately convex lines result. Both Job (1955) and Basu (1959) obtained some linear semilog relations for studies on active metabolism, from which estimates of error could be computed.

SALINITY. At the same temperature and pressure the oxygen content of a saturated solution is decreased by increased salinity, and consequently oxygen availability is affected.

The problem to the fish of maintaining osmotic balance as a demand on standard metabolism will be affected by the extent of the deviation from blood concentration (9 to 14‰). Since ionic differences exist even at equal osmotic pressure, work is performed. Studies by Hickman (1959) do not support the relation that osmotic equilibrium of blood and water salinity provides the lowest

metabolic demand in a species found in either fresh or salt water (starry flounder, *Platichthys stellatus*). Moderate changes in salinity of about 6 to 8‰ from a hypertonic to an isotonic level of 14‰ did not produce significant change. Transfer to fresh water showed a 10% decrease in standard metabolism. Similar reductions in oxygen consumption in fresh water are reported for both the juvenile and adult eel, *Anguilla vulgaris* (Raffy and Fontaine, 1930; Raffy, 1933). However, Job (1959) has reported that the marine catfish *Plotosus anguillaris* showed a definite reduction in standard metabolism when acclimated to approximately 12.5‰ (probably isotonic) after transfer from its average habitat level of 30‰. Undoubtedly, there is a complex interaction of water balance, ionic retention, tissue tolerance, irritability, oxygen transport and osmotic work involved in the final metabolic balance, which deserves critical examination.

SIZE. Size, which involves weight (wet or dry), length and surface area is of marked significance in relation to metabolism. Zeuthen (1953) and Winberg (1956) have reviewed the subject. Fry (1957) and Hickman (1959) give it special attention. In general, "heat production per unit weight in relatively mature animals of different species, as well as the same species, declines with increasing size. Consequently, we may say that the sum of enzymes, metabolites and perhaps inhibitors which govern metabolic activity grows less than the totality of the protoplasm" (Zeuthen, 1953).

The general equation $Y = a.X^b$ applies where Y is metabolism and X body weight. "*b*", the slope on a double log plot, approximates 0.80 (0.76 to 0.86) for a wide variety of fish of both freshwater and marine habitat. The parameter *a*, the rate of oxygen uptake for unit weight, shows much greater variation (0.2 to 0.5 at 20°C), which appears to be due to a combination of inherent species difference, seasonal or hormonal (maturation) differences, degree of cold adaptation (Scholander *et al.*, 1953), and measurements made which approximate routine metabolism rather than standard metabolism. Job (1955) demonstrated in the case of the speckled trout that the slope *b* for active metabolism was of the same order as that for standard rates, except that larger fish showed some decrease. Both rates showed a progressive decrease with increasing temperature.

It is entirely necessary, therefore, to quote the total weight of any organism used with considerable accuracy. Individual metabolic variation appears to be large. As reported in the literature for fish of approximately equal weight, and like circumstances, metabolic rates can differ by as much as 3 times.

Since Zeuthen (1953) quotes a similar relation to body nitrogen in many instances, there appears to be no particular choice between wet weight or body N as a basis for comparison. For increased size, if structural components (bone, cartilage, connective tissue) and fat deposits increase proportionately more than functional tissues (muscle, gland, nerve), then a corresponding decrease in metabolism per unit weight would be expected.

In a study of muscle, liver and brain metabolism in relation to body size and general activity in three species of marine fish Vernberg (1954) found a slight increase in the rate of oxygen consumption (Q_{O_2}) of toadfish brain and muscle and also scup brain with increasing body size, whereas toadfish liver showed a

decrease. Only brain Q_{O_2} showed a direct correlation with activity. Prosser *et al.* (1957) discovered that goldfish when acclimated to low oxygen showed a significant decrease in Q_{O_2} of brain and muscle but not of liver. These pertinent findings support the proposition that changes in total metabolic rate with size depend on neural and/or hormonal control rather than a change in basic tissue metabolism, but the latter can occur under conditions of reduced oxygen.

For a given species the problem of finding a common basis for comparing respiration of different body weights cannot as yet be resolved by any other method than that of empirically determining the slope "*b*" from a sufficient sample to provide a reliable estimate of variability.

STARVATION. As noted earlier, the change in R.Q. which must accompany the long starvation of migrating mature salmon would reflect in some change in oxygen uptake per unit of work, since body fat is virtually oxidized away. Also, the body-weight changes which inevitably accompany the loss of fat and periods of uptake or loss of water would support the need for relating metabolism to body nitrogen.

Standard metabolism has been shown to decrease by $\frac{1}{2}$ to $\frac{1}{4}$ of the non-starved rate in 7 to 300 days. Rapid decrease characterized the early phases of starvation, which Hickman (1959) found in the starry flounder to follow a logarithmic rate of decay. If not considered, or food has been inadvertently denied the experimental fish, the error component appears to be of the order of 10% difference between the rate for a starvation period of 24 hours and that for 48 hours. Active metabolism in speckled trout showed no such change (Fry, 1957) which may prove a considerable asset in establishing reliable estimates for active fish.

ACCLIMATION. Fully acclimated fish are required (temperature, pH, salinity, oxygen content and possibly pressure). Both the level of acclimation and the process of acclimation can affect the rate of metabolism. Rates of metabolic acclimation seem to be unrecorded. Those for temperature (Brett, 1946) and oxygen (Shepard, 1955; Prosser *et al.*, 1957) show periods for completion ranging from 1 to 20 days, the latter for low temperature.

SEASON. Elevated or reduced levels of the above environmental entities can act as stimulating or depressing factors. It is unusual for experiments in recent times to be conducted without due regard to acclimation. There is, however, the problem of season in which such "priming" factors as changing day-length or increasing temperature when coupled with appropriate stages of development may stimulate the endocrine system (cf. Roberts, 1960; Evans *et al.*, 1962). Metabolic rates related to racial behaviour in an arctic whitefish (resident and migratory forms), and to season in the bluegill, have been found to show significant differences when body weight, temperature and activity are taken into account (Wohlschlag, 1957; Wohlschlag and Juliano, 1959). Differences of the order of 30% existed between the whitefish races. Winter metabolic rates in the sunfish were higher for comparable temperatures and swimming rates than those in spring and autumn.

EFFICIENCY AND UNIT OF PERFORMANCE

Throughout almost all these studies it is only indirectly possible to determine the demand for the most common activity of all, *locomotion*. Activity meters measure disturbance of water, which results from any and all forms of undefined movement. Active metabolism has usually been produced by stimulating the fish to swim at a maximal rate, but the swimming speed itself has not been accurately measured. Indeed, Fry and Hart (1948) remarked that "the values obtained for cruising speeds are estimates rather than absolute measures". In the case of young coho and sockeye, Brett *et al.* (1958) showed clearly the presence of excessive activity followed by slumps in performance, during the first hour of swimming-speed tests, which undoubtedly were involved with oxygen debt and its replacement. Active metabolism is definitely produced by, but may not be directly related to, performance in the early stages. Basu (1959) includes a table which shows no relation between oxygen consumption and revolutions per minute of his annular respirometer, although it increased in rate from 5 to 30 rpm. The effect of adding an electric field almost doubled the metabolic rate independent of swimming speed. Apparently the excitement of the circumstances was so great that even though performing little locomotory work at low rates of rotation the fish was respiring maximally. Since active metabolism was the chief interest, the odd circumstances were inconsequential to the experiment. Wohlschlag (1957) used a circular chamber rotated at "whatever velocity the fish would tend to swim". The maximum difference in path which a fish could follow from the mean path was approximately 35%. Although excitement did not appear to characterize his fish, any spontaneous activity would bias results in the direction of increased demand. One "repeated" whitefish, despite slightly decreased rotation rate, consumed 50% *more* oxygen than on the initial run. In general, however, only 25% of the variance in the oxygen uptake was not accounted for by the variables of weight, rotation rate and temperature.

In order to determine the instantaneous energy demand of locomotion, it is obvious that accurate measures of metabolism for equally accurate swimming speeds at all levels of capacity, free from the involvement of oxygen debt or unusual excitation, must be obtained. The problem is not insuperable though it does appear involved.

There is yet another intriguing aspect, one which concerns the efficiency of swimming as a process of performing the necessary work to overcome hydrodynamic friction. Gray (1957) has implied that on the basis of the drag imposed on equivalent hydrofoils, salmon have not enough stored energy to reach distant spawning grounds. This intentionally contradictory statement, sometimes referred to as "Gray's paradox", points up the present lack of understanding of the drag forces on a flexing streamlined form. The work of Bainbridge (1958, 1960) appears to offer an intermediate stage while the students of hydrodynamics resolve the paradox (see further: Bainbridge, 1961; Kent *et al.*, 1961).

By studying the tail-beat frequency in a variety of fishes, including such streamlined forms as dace and trout, Bainbridge (1958) has shown that with the

exception of frequencies below 5/sec there is a direct relation between velocity (V), total length (L), and frequency (f) expressed by the equation $V = 0.25[L(3f - 4)]$. At lower frequencies the amplitude of the beat decreases.

Data obtained to date for a variety of species indicate that maximum sustained speed varies directly as body length, to a first approximation. Hence, by expressing the swimming speed in terms of body lengths traversed per unit time, a basis for imposing given work loads on fish of different lengths within and between species could be employed. Therefore, if the energy required to propel a fish *1 body length in 1 second* were determined, the relative efficiencies could be obtained without knowledge of the actual physical work performed. This would, however, only provide a first order of accuracy since some fishes change their body proportions with growth, and others alter their means of propulsion from sculling with pectoral fins to thrust from caudal fin.

Even as an empirical basis for comparison of metabolic rates, it would be more precise than that for the inevitably vague routine rate. Among those species reported by Bainbridge (1960), and from recent tests conducted on young and adult sockeye salmon (Brett, MS 1962), velocities of 3.5 to 4.2 Lengths/sec represent 1-hour maximum sustained speeds. If the relation between oxygen consumption (mg/kg/hr) and velocity (L/sec) is semilogarithmic with a slope of 0.3, as indicated in our preliminary studies, a speed of 1 L/sec would require about one-fifth of the maximum rate of oxygen uptake.

CONCLUSIONS

Much remains to be done in the study of fish metabolism. Assumptions from mammalian physiology are frequently but not always justified. In particular the energy demands of all forms of activity need adequate determination.

Rate of oxygen consumption is subject to a great many factors including activity, oxygen availability, oxygen debt, carbon dioxide, ammonia, hydrogen-ion, temperature, salinity, size, starvation, acclimation, season, sex and condition. Some of these entities have a potential capacity for altering the rate by 5- to 10-fold, imposing the need for scrupulous attention to experimental approach before systematic, reproducible measures can be obtained.

At present the efficiency of energy expenditure in locomotion defies assessment since accurate estimates of energy demand for known drag force have not been obtained. As a provisionary basis for comparison among streamlined fish of salmonoid form the energy required for propulsion at a rate of *1 body length per second* and multiples thereof is suggested.

ACKNOWLEDGMENTS

This was written following an invitation in 1960 from Dr S. V. Job, University Zoology Research Laboratory, Madras, India, to submit a paper of broad scope concerning some major topic in fisheries research for inclusion in a commemorative volume. Unfortunately, the proposal had to be abandoned. I remain indebted to Dr Job for the suggestion and criticism of the manuscript.

Further, it is a pleasure to acknowledge many profitable discussions with my associates Drs D. F. Alderdice, G. R. Bell and W. E. Vanstone during the compilation.

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An Improved Method for the Preparation of Fish Protein Concentrate from Cod[1]

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ABSTRACT

A high quality fish protein concentrate can be produced from cod fillets by extraction with suitable isopropanol–water mixtures. A process has been developed, on a pilot plant scale, for the production of high quality fish protein concentrate from skinned cod fillets by this method. It is white in colour and of soft texture and for all practical purposes tasteless and odourless. The analysis on a moisture-free basis, of a typical sample shows the following protein (N × 6.25), 96%; ash, 5%; lipids, 0.033%. The moisture remaining in the product after drying is approximately 4%. The yield of protein concentrate (approx. 4% moisture) is between 12 and 15%.

INTRODUCTION

One of the most pressing problems faced by the world today is the one of feeding the peoples of the various nations in such a manner as to keep them healthy and strong. Unfortunately most countries are not as fortunate as the countries of the North American continent and Europe in their supply of food. In underdeveloped and underprivileged countries the diet of the ordinary man is seriously deficient in several factors. Of these, the inadequacy of the protein portion of the diet causes serious difficulties. Meats are in short supply, and fish, even though nearby waters may contain large quantities, are not readily available. This may be due to the rapid spoilage which occurs in fish when refrigeration facilities are not available, as well as a lack of knowledge and facilities for catching large quantities of fish. In some areas of the world the people are prevented from making full use of fish as a food through local prejudices, taboos and customs. Often the proteins that are available from the vegetable matter in their diets do not supply them with all the required amino acids necessary for a healthy diet. The result of this is that some of the people of these countries suffer from failure of growth, muscular wasting, oedema and other symptoms of such diseases as "kwashiorkor" and "marasmus" to which protein deficiency in the diet contributes. The addition of 10% fish protein concentrate to white bread has been shown to effect improvement in the protein efficiency ratio of the order of 82 to 198% (Morrison and Campbell, 1960).

With the population of the world increasing each year, protein malnutrition can only become more serious unless some solution is found. Fortunately, hope of an eventual solution to the problem is given in the development of a substance known popularly as "fish flour". Since this material contains little or none of

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the carbohydrates and starches of wheat flour but contains up to 96% protein, a more descriptive name would be "fish protein concentrate". This protein concentrate as prepared by the method of Guttmann and Vandenheuvel (1957) and brought to pilot plant stage by Gunnarsson *et al.* (1958), has been shown to be an excellent source of high quality protein (Morrison and Campbell, 1960; Larsen and Hawkins, 1961). A small quantity of fish protein concentrate added to the protein deficient diets of the some 500 million people who suffer from protein deficiency should result in a major improvement in the health of these people.

Because of a renewed interest in the use of fish protein concentrate by the United Nations and other groups for use in aiding underdeveloped nations, it was decided to investigate the possibilities of developing an improved process for producing fish protein concentrate from cod muscle. Since the original work done on isopropanol-extracted fish protein concentrate (Guttmann and Vandenheuvel, 1957), our knowledge of the extraction of lipids and water-soluble material from fish muscle has been greatly increased (Dambergs, 1956; 1959). From work by Dambergs on small samples of fish it was thought possible to eliminate the cooking stage used in the Guttmann–Vandenheuvel procedure which occasionally gave trouble during processing. A more consistent colour and texture was also desired.

EXPERIMENTS AND RESULTS

Experiments were carried out, using 50-lb batches of untreated market cod fillets, to evaluate various extraction procedures with 70:30 (v/v) isopropanol–water mixtures (Dambergs, 1959) designed to give the most efficient extraction of both lipids and water-soluble materials. All extractions were carried out by batch operation in a 30-imp gal steam-jacketed stainless steel reaction kettle with mechanical stirrer. The extract was removed by a basket centrifuge and the final material dried in a shelf-type air dryer at 100 to 110°F. The quality of the finished concentrate was determined generally by organoleptic tests and more specifically by reflectometric measurements and chemical analyses.

Analytical Methods

Water. Samples of 10 g were dried to constant weight in an LKB moisture tester by means of an infrared heater.

Fat. Samples of 25 g were extracted according to the chloroform–methanol phase separation method of Bligh and Dyer (1959) adapted for use with dry materials.

Ash. Samples were ignited to constant weight at 550°C.

Total nitrogen. The Kjeldahl–Gunning–Arnold method (A.O.A.C. 1955) was employed using 1-g samples.

Protein. Nitrogen × 6.25.

Colour. Samples of compressed protein concentrate were measured for percent reflectance between 390 and 510 mμ by means of a Beckman model DU spectrophotometer fitted with a diffuse reflectance attachment.

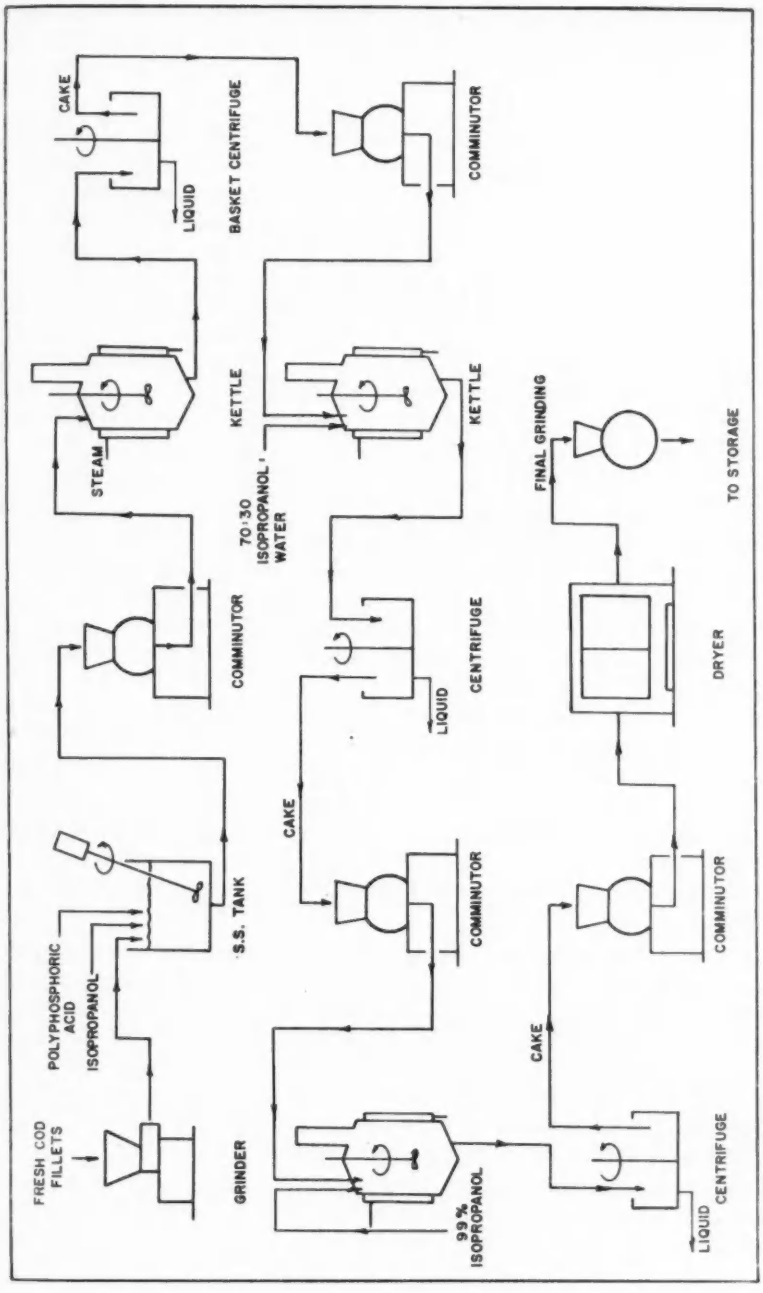

FIG. 1. Flow diagram for production of fish protein concentrate.

A very satisfactory product was obtained using an extraction procedure involving two hot (178 to 180°F) extractions with 70:30 isopropanol–water, followed by one hot extraction with 99% isopropanol. This procedure, shown in Fig. 1, is outlined below.

STEP I. Fresh, skinned cod fillets are ground to ¼-inch size in a 1½-hp meat grinder. Sufficient 99% isopropanol is added to give a 70:30 isopropanol–water ratio in the mixture making use of the water already contained in the muscle. This requires approximately 19 imp gal of 99% iospropanol per 100 lb of fillets. The mixture is stirred for 15 minutes in a stainless steel tank, during which time sufficient 20% polyphosphoric acid is added to bring the pH to 5.5. This partly hydrolyzes the connective tissue making the collagen and gelatin more soluble. The flesh of this fillet is dehydrated and slightly denaturated by the alcohol. The texture of the flesh changes from a soft paste to granular particles and makes possible the use of a high speed comminutor for further size reduction. The alcohol–fillet mixture is then put through a Fitzpatrick comminutor fitted with a screen having ⅛-inch diameter holes.

STEP II. The material is then put in a 30-gal reaction kettle and maintained at 178 to 180°F with constant agitation for 30 minutes. A glass reflux condenser is used to prevent loss of alcohol. The material is then pumped to the Bird Basket centrifuge and the liquid centrifuged off. The cake then contains 45 to 50% liquid. At this point approximately 94% of the fat and 72% of the water solubles which will be removed, have been extracted. The cake is then broken up by passing it through the Fitzpatrick comminutor, this time fitted with a screen having ½-inch square openings.

STEP III. The shredded cake is replaced in the reaction kettle with 10 gal of 70:30 isopropanol–water mixture for each 100 lb of starting material. The temperature of the mixture is raised to 178–180°F and held there for 15 minutes with constant agitation. It is then pumped to the Bird centrifuge and the liquid removed. After this extraction approximately 97.5% of the fat and 98% of the water-soluble material which will be removed has been extracted. The cake is again shredded in the Fitzpatrick comminutor using the screen with ½-inch square holes.

STEP IV. The material is then put in the reaction kettle with 99% isopropanol and again heated at 178–180°F for 15 minutes while being constantly agitated. In this extraction 10 gal of isopropanol are used per 100 lb of starting material. The slurry is then pumped to the centrifuge and the liquid centrifuged off. A further 4 gal of 99% isopropanol is then placed in the kettle and heated to 178–180°F and then pumped into the centrifuge in order to clean the last of the solids from the kettle, pump, and lines, and to wash the cake in the centrifuge. The cake is then broken up in the Fitzpatrick comminutor.

The fat content after the extraction will be less than .06% (usually from .016–.04%) on a dry basis as measured by extraction with a methanol–chloroform mixture (Bligh and Dyer method). Extraction by ether in a soxhlet apparatus shows a smaller fat content.

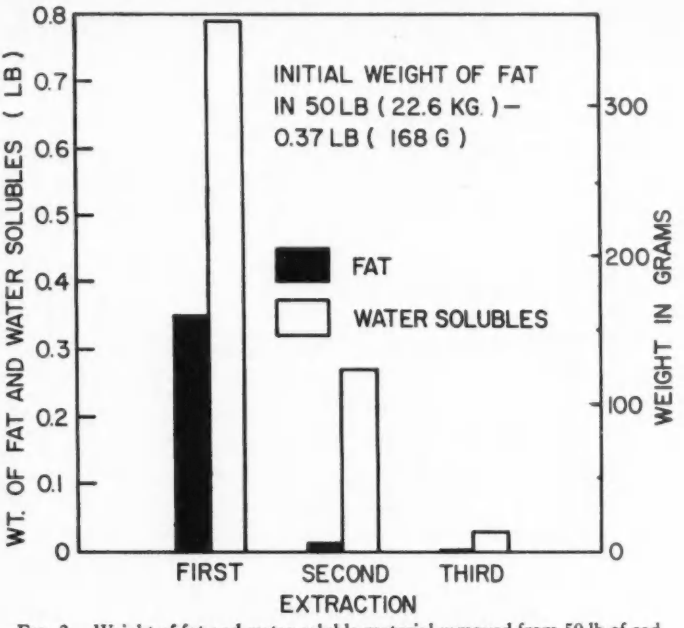

FIG. 2. Weight of fat and water-soluble material removed from 50 lb of cod fillets during conversion to fish protein concentrate.

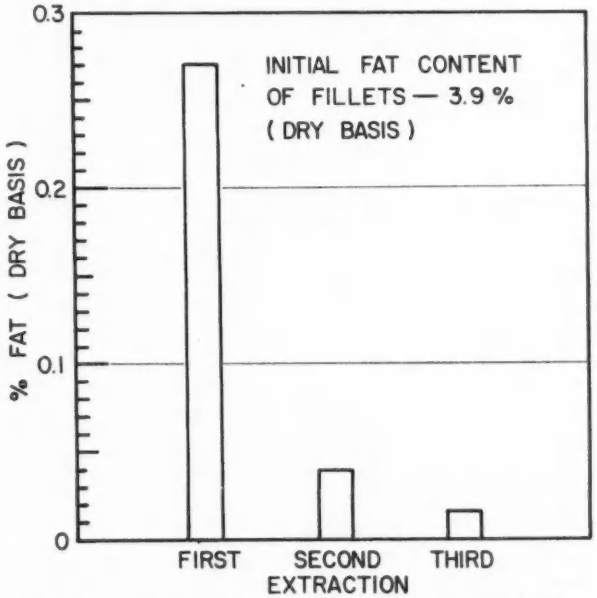

FIG. 3. Percent fat remaining in fish protein concentrate after first, second and third extraction.

STEP V. The ground cake is then dried in trays using a cabinet-type dryer in which air at 100–110°F is blown over the trays of material. Drying takes from 24 to 36 hours depending on local weather conditions. The alcohol is removed and the moisture reduced to 3–4%.

The effect of each extraction in terms of fat and water-soluble material removed from the fish and of fat remaining in the material is shown in Fig. 2 and 3. Fig. 4 shows the diffuse reflectance curve for the concentrate after processing is completed.

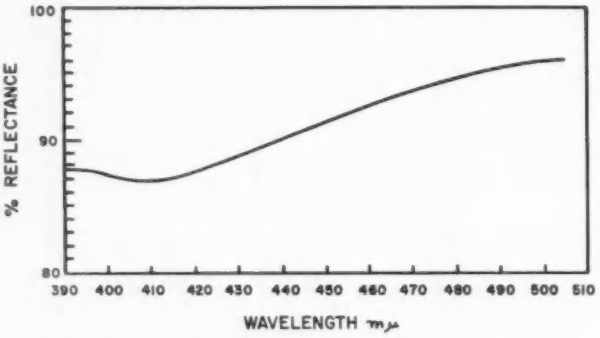

FIG. 4. Typical diffuse reflectance curve for fish protein concentrate prepared from cod fillets.

TABLE I. Capacity of pilot plant equipment.

Operation	Material	Equipment	Capacity of equipment
Grinding	Fillets	Hobart meat grinder model 4332 1½ hp	1500 lb fillets/hr
	Fillets and isopropanol	Fitzpatrick comminutor model D ¼-inch openings in screen	760 lb/hr (equivalent to 370 lb fillets/hr)
	Damp fish protein concentrate (45 to 50% liquid)	Fitzpatrick comminutor model D ½-inch openings in screen	660 lb/hr (equivalent to 3000 lb fillets/hr)
	Dried fish protein concentrate	Reitz disintegrate model RA-4-K53	155 lb/hr dry protein concentrate from dryer (equivalent to 1300 lb fillets/hr)
Centrifuging	Extracted fillets	26-inch Bird basket centrifuge two speed: 900 and 1800 rpm	192 lb damp cake/hr including unloading time (equivalent to 530 lb fillets/hr)
Extraction	Fillet–isopropanol mixture	30-imp gal steam-jacketed, stainless steel reaction kettle with stirrer	275 lb/hr (equivalent to 133 lb fillets/hr)
Drying	Damp fish protein concentrate (45 to 50% liquid)	Cabinet dryer, 48 sq ft tray area; tray loading, 2 lb/sq ft	3.7 lb damp cake/hr (equivalent 12.5 lb fillets/hr)

After drying, final grinding to flour size is performed in a Reitz disintegrator using a .032-inch screen. The final product is then sealed in polyethylene bags.

The capacities of the various pieces of equipment used in the preparation of the experimental batches are given in Table I. The capacity of each unit is given both for the material on which the operation is performed and also in terms of the equivalent weight of original fillets.

CONCLUSION

This procedure was found to yield a white concentrate very high in protein and for all practical purposes odourless and tasteless. The texture was soft, resembling wheat flour. Proximate analysis of a typical sample would show the following composition:

Moisture	4%
Ash	5% (dry basis)
Lipid	.033% (Methanol–chloroform extraction, dry basis)
Protein (N × 6.25)	96% (dry basis)

The yield of fish protein concentrate, using 50-lb lots of fillets and batch processing was between 12% and 15%. However, in commercial production, handling losses could be reduced and the yield increased.

ACKNOWLEDGMENTS

The author would like to extend his thanks to Mr C. A. Campbell for his assistance in the preparation of the fish protein concentrate samples and Mr N. Dambergs for his valuable advice.

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Aggressive Behavior in Juvenile Coho Salmon as a Cause of Emigration[1]

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ABSTRACT

Large numbers of coho fry (called nomads) move downstream from shortly after emergence through early fall. These fry are smaller than residual coho. Study of behavior showed coho to be aggressive and territorial or hierarchical. Nomadic coho placed in stream aquaria barren of resident fish tended to remain in the aquaria rather than continuing downstream movement, while nomads added to resident groups of coho were dominated by the resident dominant fish and tended to leave the channels. Hierarchies were organized on the basis of fish size, with larger fry having better growth opportunities. Feeding of coho in excess of requirements did not alter holding capacity of stream aquaria. Aggression observed in natural stream areas was frequent, probably virtually continuous. Nomads transferred to natural stream areas barren of other coho remained there, while nomads added to resident populations tended to move downstream. It was concluded that aggressive behavior is one important factor causing downstream movement of coho fry.

INTRODUCTION

This paper reports a study of aggression in coho salmon (*Oncorhynchus kisutch*), showing that downstream movement of coho fry is an important result of aggressive behavior.

Several workers have recorded extensive emigrations or downstream movements of coho fry in the spring subsequent to the emergence of fish from the spawning gravel (Salo and Bayliff, 1958; Oregon Fish Commission, 1958; Chapman *et al.*, 1961; and unpublished studies at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.). The downstream movements of fry usually begin soon after emergence and continue through early summer. This downstream fry migration, coupled with the concepts of behavior developed by several workers, suggested that the aggressive behavior of certain dominant individuals in the coho population was one stimulus leading to the observed downstream migration.

Aggressive behavior has been found to be a significant mechanism of intraspecific competition and is regarded as a factor important in the ecology and sociology of natural animal populations (Collias, 1944). Territoriality in stream-dwelling salmonids, apart from reproductive behavior, has been suggested to be a characteristic evolved as a function to assure adequate food supply (Kalleberg, 1958) and a factor promoting wide distribution of the fish in streams (Hoar, 1951).

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Aggressive behavior of eastern brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) has been shown by Newman (1956), who observed formation of social hierarchies as well as territoriality. Kalleberg (1958) showed that brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) were strongly territorial. These species developed a mosaic of territories in aquaria. Increase in population density beyond saturation caused some individual territories to completely disappear rather than adjusting by the compression of the living area of less aggressive fish. Hoar (1951) reported territorial behavior in coho

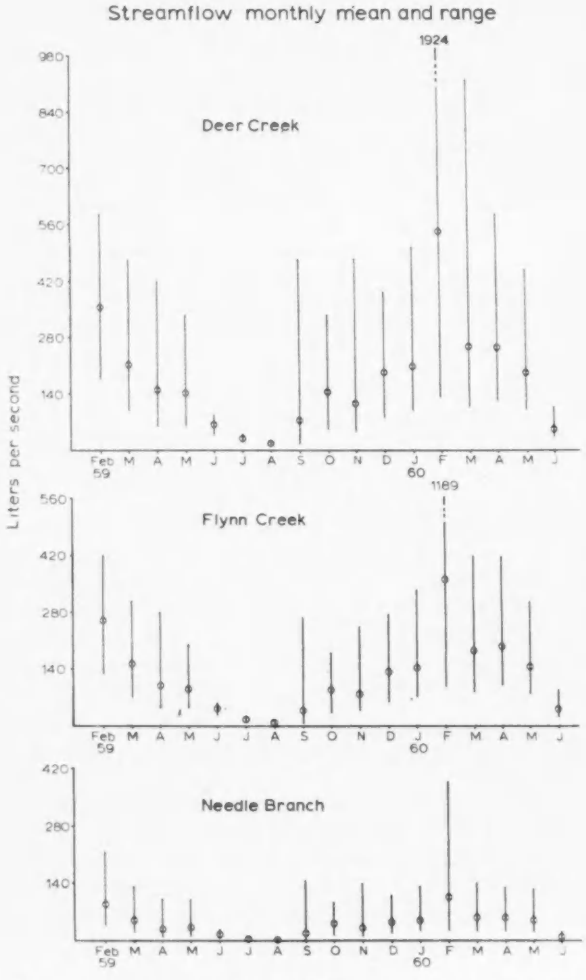

FIG. 1. Streamflow monthly mean and range in liters per second, February, 1959 to July, 1960.

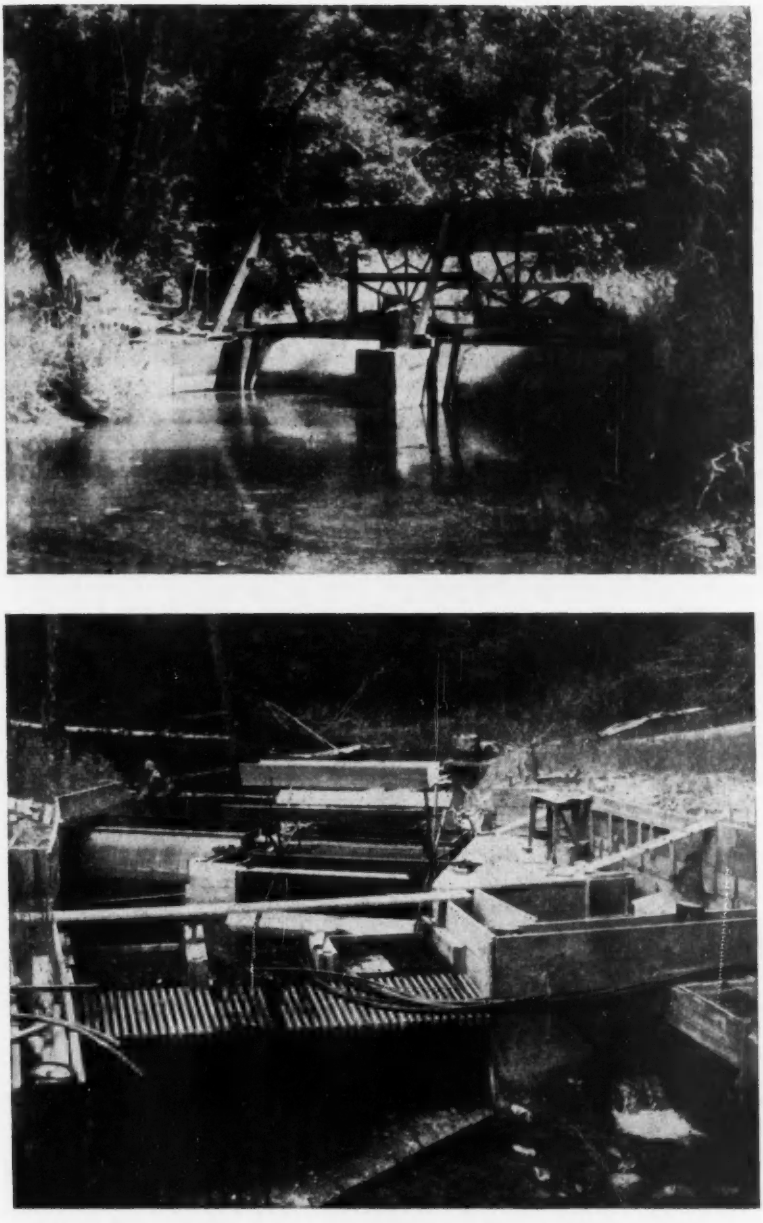

FIG. 2. *Above:* upstream view of the traps used at Flynn Creek; *below:* downstream view of the traps at Deer Creek.

salmon fry, stating that coho fry maintain definite positions relative to certain objects in their environment, and tend to remain in slower flows and to be quiet at night. Hoar felt that these traits prevent downstream displacement of fry.

Downstream movement of fry can, of course, be attributed to one or more possible factors: displacement by current, innate tendency to migrate (apart from movement enforced by aggression), random shifts in position, or aggression (such as territorial behavior) within the fry population. The principal hypothesis tested in this paper was that the downstream drift of coho fry was caused primarily by aggressive behavior of residual coho. Work was conducted from April, 1960, to November, 1961.

DESCRIPTION OF STUDY AREA

Most of the research reported here was conducted on three tributaries (Deer Creek, Flynn Creek and Needle Branch) of Drift Creek, the latter stream draining into Alsea Bay near Waldport on the Oregon coast. The streams are about 4.0 km, or less, apart, and their seasonal changes in biotic and physical characteristics are parallel. The three streams are described in another paper (Chapman *et al.*, 1961). Figure 1 shows stream flow in each stream, demonstrating that great seasonal variability in flow occurs.

Salmonid fishes present in the streams are coho salmon, coastal cutthroat trout (*Salmo clarki clarki*), and steelhead trout (*S. gairdneri*). Coho salmon are

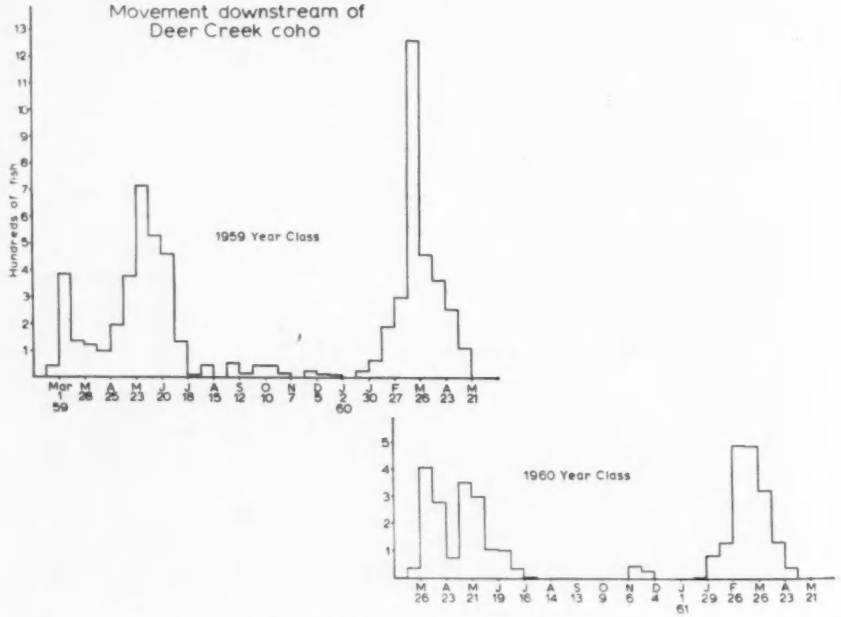

FIG. 3. Downstream movement of juvenile coho salmon in Deer Creek, 1959 and 1960 year-classes.

the most abundant of the three species. Data on upstream and downstream movements were collected by means of fish traps on the three streams. The trap used on Deer Creek is shown in Fig. 2. Virtually all fish moving upstream and downstream are taken in the traps. Available data on downstream movements of coho are shown in Fig. 3 and 4 in order to give some idea of the importance of the downstream drift of fry in the first few months of life. Coho fry moving through downstream traps from time of emergence through October are termed "nomads" in this paper. Coho moving downstream after October are called migrants or smolts.

METHODS

The means used to test the principal hypothesis were of necessity indirect. Nomads were placed in artificial stream sections, both test and control, constructed in observation troughs, and observations were made of their behavior and interaction with coho resident in the sections. Test sections contained a resident group of coho while control sections were barren of resident fish.

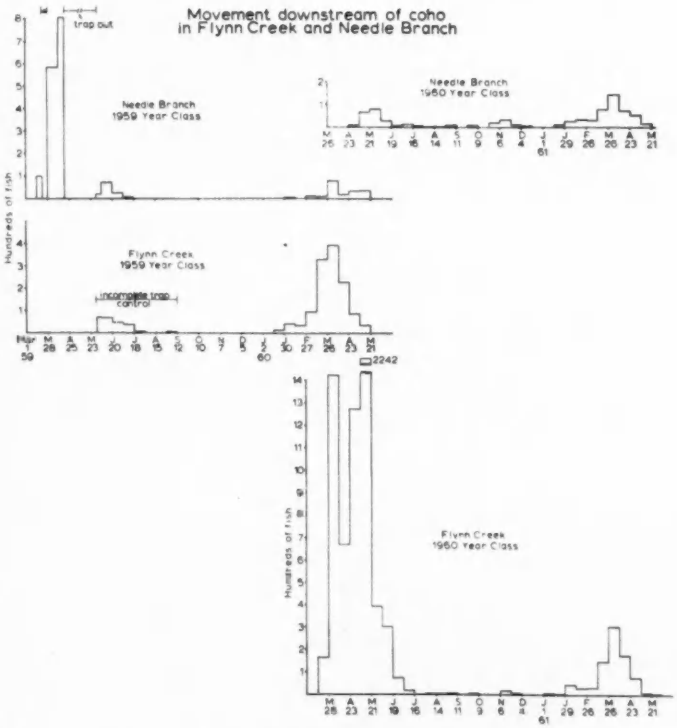

FIG. 4. Downstream movement of juvenile coho salmon in Flynn Creek and Needle Branch, 1959 and 1960 year-classes.

Nomads were also placed in a controlled natural stream area or stream from which resident coho had been removed. Both methods tested the theory that nomads would cease movement downstream if given adequate living space. Nomadic coho should not remain in observation channels or in controlled natural areas if their movement was due to their displacement by strong water current or innate tendency to migrate. In addition to the two experimental methods of testing the hypothesis, supporting evidence was gathered through the observation of coho behavior and sampling of growth of nomadic and residual coho fry in the study streams.

Artificial Channels at Deer Creek

Two troughs (Fig. 5 and 6), each consisting of paired channels, were constructed at the downstream end of the Deer Creek fish trap. Water for troughs was passed through plastic pipe leading from the pool above the fish trap dam to the trough forebays. Flow through each A channel was about 10.6 liters per minute; through each B channel it was 15 l/min in 1960 and 95 l/min in 1961.

The bottoms of all 4 channels were built up by addition of natural stream bottom materials so that each channel in 1960 had 2 pools and 3 shallow areas or riffles. Invertebrate forms were present in the material placed in the troughs,

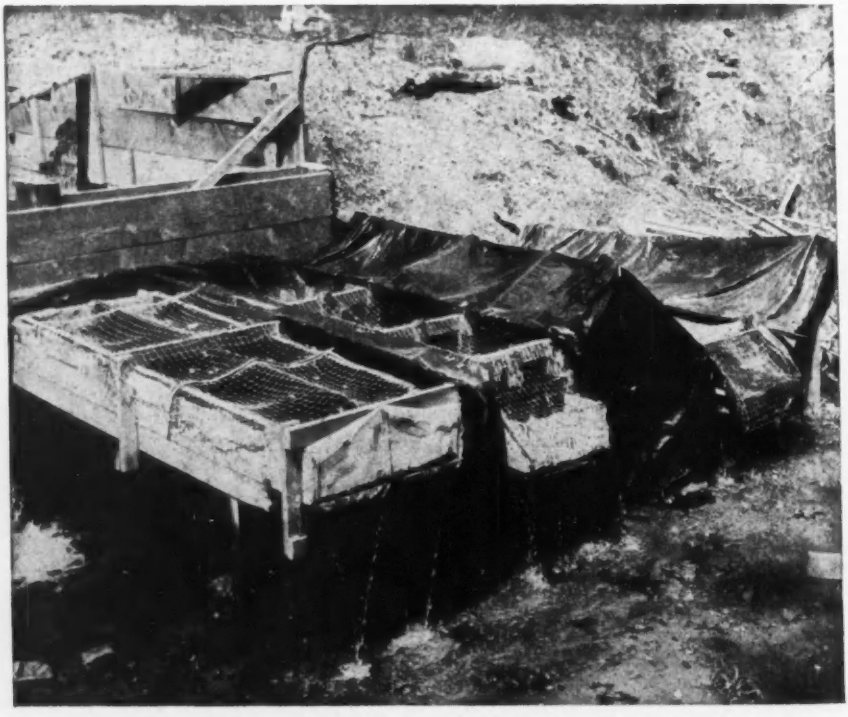

Fig. 5. Artificial stream channels at Deer Creek used for study of coho behavior.

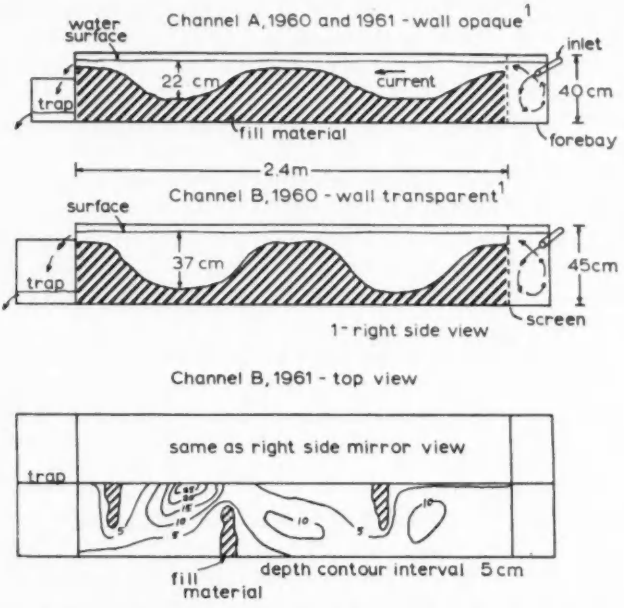

FIG. 6. Schematic drawing of artificial channels at Deer Creek.

and additional insect larvae were added before fish were placed in the troughs to help insure an adequate supply of insect forms used by coho (Demory, MS, 1961). An abundant algal growth, largely *Oscillatoria* sp., became established soon after the troughs were constructed. In 1961 the channels were altered so that 3 shallow pools and 3 riffles were created (Fig. 6) in each channel. Water was maintained in the A and B channels through the winter of 1960–61 so that an invertebrate population was established and present during 1961 experiments.

Twine netting having a mesh of 38 mm from knot to knot was placed over all 4 channels to prevent birds from preying on experimental fish, and to provide some cover. Benches were placed at the sides of the B channels, and black polyethylene canopies or tents were placed over benches so that fish looked out upon a dark area.

No coho could pass the screening between forebays and observation channels. Any coho placed in the channels had to live there, die there, or pass downstream into inclined plane traps from which they could not escape.

During part of the 1960 studies with troughs A and B, the fish were fed. Adult brine shrimp, *Artemia* sp., were frozen in 1-gram lots in ice cubes and used according to a feeding schedule. The quantity of food fed was determined from coho growth data obtained by personnel of the Fish and Game Management Department at Oregon State University. These data indicated that maximum growth of coho was induced by a ration of about 150 mg (wet weight) of amphipods daily per gram of fish tissue. Therefore a daily ration of about 300 mg of brine

shrimp per gram of fish tissue was fed to assure an excess of available food. The food cubes were placed at the upper end of each channel in wire baskets placed in the water. As the cubes melted, the shrimps drifted downstream. Experimental coho, 35 to 65 mm, fed avidly upon these shrimps. Fish were fed twice daily early in the work, then once daily as it became evident that this was adequate.

Nomads for artificial channel experiments were obtained from the Deer Creek downstream trap, and measured and marked by a notch in one of the fins. Fish for experimental use were selected randomly if more than the number required were in the trap. After being held in plastic buckets for 15 minutes to permit recovery from handling, the coho were placed in the channels at the upstream ends.

In initial experiments the capacities of A and B channels were determined by means of introductions of nomads into barren channels. When capacities had been determined approximately, groups of 3 to 5 coho were placed at the same time in each channel. One group of nomads was added to a resident group of coho in the test channel while another introduced group was added simultaneously to the barren control channel.

In the test channel a resident group of coho was established, and these fish formed the population to which new nomads were added. In the second channel, designated as a control, all coho were removed before new groups of fish were introduced. The test and control channels were essentially alike except that the test channel contained a resident group of coho.

In several experiments the resident coho were removed from the test channel, measured (fork lengths), and in all respects handled in the same manner as nomads to be introduced. Observation of subsequent behavior patterns and test results revealed no difference between behavior of resident coho handled in this manner and those not handled at all.

In some experiments late in August and September, 1960, resident coho seined from a stream area were used, since no nomads were available at that time.

Artificial Channels at Oak Creek

A pair of artificial stream channels was constructed at Oak Creek, 5 miles west of Oregon State University, for long-term study of coho behavior. The paired channels are shown in Fig. 7.

The bottom of the channels was built up with gravel and sand to the level of the window bottoms, and the final surface layer at that level was flat, smooth, and composed of rock particles about 3 mm in diameter.

Flow in each channel varied from a maximum of 227 l/min to a minimum of 114 l/min, depending on the head of water in the source stream. Depth in the channels decreased as stream flow decreased, from 51 mm to a minimum of 25 mm.

The channels were exactly alike in all possible respects: depth, bottom type, current, total flow, overhead cover, and surroundings. All channel wood parts were painted a dull brown to simulate soil coloration. Tents were constructed

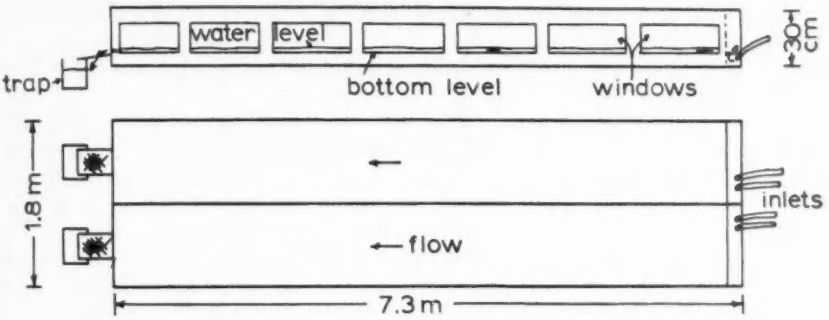

FIG. 7. Schematic drawing of artificial channels at Oak Creek.

on the sides of the channels so that experimental fish looked out upon a dark area beyond the channel windows. The tents also hid movements of observers.

Fish placed in the channels had free access to the exit orifices and could leave the channels at will, but could not return. Nomads used in the Oak Creek channels were transferred there from the downstream migrant trap at Deer Creek.

Fish in both channels were fed once each day with brine shrimps in the same manner as described for the Deer Creek observation channels. Daily ration was 300 mg of brine shrimps per gram of coho tissue.

CONTROLLED STREAM SECTION

A controlled stream section (Fig. 8) 18 m in length was formed by screens in Deer Creek, with the upstream end of the section about 91 m below Deer Creek trap. A downstream trap was placed at the lower end of the stream section and a by-pass constructed so that migrating fish could move around the controlled section, either up or downstream.

All resident coho were removed from the controlled section by electrofishing before experimental fish were added. Trout and cottids taken in this operation were returned to the controlled section, which was operated from early July to mid September, 1960.

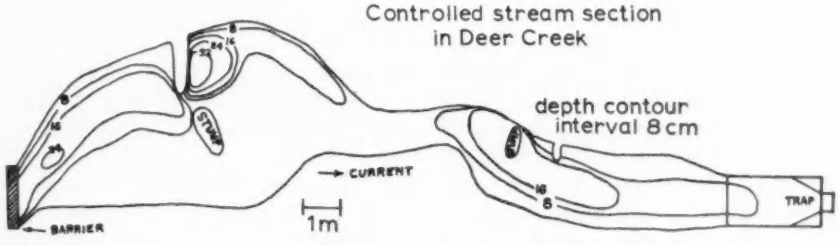

FIG. 8. Controlled stream section in Deer Creek.

Nomads were secured in the downstream trap at Deer Creek, then marked and handled as in artificial channel work. These fish could live in the controlled section, die there, or pass downstream into the trap at the end of the section.

There were about 39 m^2 of stream area in the section, of which about 83% was 25 mm or greater in depth. The controlled section was not unlike many other Deer Creek stream areas in general appearance.

Transfer of Fry to Barren Stream

A transfer of 1627 coho nomads from Flynn Creek to Needle Branch was made from April 16 to May 6, 1960. No coho fry were present in Needle Branch at the time of this fry transfer because of failure of the adult coho run of the previous fall. The transfer provided a further test of the idea that nomads would become residents if living space were available. The transferred coho were released in small lots through the available stream area on Needle Branch.

A transfer of 1577 coho nomads from Flynn Creek to Needle Branch was made from April 19 to May 4, 1961. Coho fry were present naturally in Needle Branch at time of transfer. The coho were released as they were in the previous year. The object of this release was to determine if the natural population already present in Needle Branch would result in a smaller proportion of the introduced nomads becoming resident than had been the case in 1960.

Observation of Coho Behavior

Observations of aggressive behavior among coho resident in natural stream areas were made on Deer Creek. The total numbers of observed nips were recorded. These observations were made on areas of known size for given time intervals, usually 10 or 20 minutes. The areas used for observation were not randomly chosen, but were selected for the visibility they afforded. An effort was made to watch deep as well as shallow areas.

In addition, observations of behavior were made while nomadic coho were in the artificial channels described earlier. For the most part these were qualitative, but some counts of nips were recorded. Care was taken to avoid sudden movements that might startle the experimental fish, but coho in the glass-walled channels usually ignored all movement outside the channels below the level of the water surface. Any movement above the water obviously frightened the fish.

Growth of Coho

Comparisons were made of growth of dominant and subordinate coho in artificial channels in several time intervals, measured as fork length. Where growth percentages in periods of time are used, these were calculated as the ratio of change in length to initial length, multiplied by 100.

Comparisons were made of mean size of nomadic and residual coho at given times. Residual fish were sampled by seining and direct-current electrofishing throughout the stream length available to coho. Nomads for length measurements were obtained from downstream traps.

RESULTS

Description of Behavior Patterns

The social behavior patterns of coho salmon were observed in artificial stream channels and natural stream areas. The behavior and resultant phenomena noted included lateral display and parallel swimming (Kalleberg, 1958), dominance posturing (Jones and Ball, 1954) or threat (Stringer and Hoar, 1955), nipping (Hoar, 1951), chasing or driving (Stringer and Hoar, 1955; Greenberg, 1947), flight, hiding, fighting (Stringer and Hoar, 1955; Newman, 1956), submission (Newman, 1956; Braddock, 1945), territorial defense (Kalleberg, 1958), redirected aggression, and formation of hierarchies (Greenberg, 1947). All of these activities except hiding, fighting, redirected aggression and hierarchy formation were observed in the stream coho population as well as in aquaria.

Lateral display (Fig. 9) in the coho is similar to that described by Kalleberg (1958) for Atlantic salmon, consisting of erected dorsal and anal fins and an open mouth. The white-edged dorsal and anal fins were most obvious in displays.

Lateral display was seen during the period of hierarchy establishment in aquaria, during territorial defense in aquaria and stream, and sometimes during the course of hierarchical dominance activities in the aquaria. Lateral threat may be a mutual vigorous display between a pair of coho, and sometimes results in parallel swimming (Kalleberg, 1958). It appears to be of defensive character.

Dominance posturing, or threat, (Fig. 10) in the coho is apparently quite similar to that of the Kamloops trout, *Salmo gairdnerii kamloops* (Stringer and Hoar, 1955). Threat was seen very frequently in aquaria when social hierarchies were being established, and in the stream and aquaria during territorial defense. It can have either defensive or offensive character.

Nipping in coho (Fig. 11) has been described by Hoar (1951). Nipping, after the initial contest for dominance, usually was incomplete, with little actual body contact.

Fighting, as described by Stringer and Hoar (1955) for the Kamloops trout, and by Newman (1956) for rainbow and eastern brook trout, was seen in the behavior of coho in aquaria during establishment of dominance–subordination relationships.

Submission without flight in the coho (Fig. 12) is similar to that observed in eastern brook trout and rainbow trout (Newman, 1956). Submission by flight was frequently seen, especially after dominance relationships were well established. Subordinate fish were often driven rapidly about the aquaria until they found a hiding place.

Redirected aggression was frequently evidenced by aggressive dominant fish when a chased subordinate suddenly disappeared by hiding under a rock. The aggressor repeatedly was seen to pick up algal tufts and spit them out. Subordinate fish, when repeatedly nipped by aggressive coho, apparently were unable to, or afraid to, nip in return and apparently transferred the aggressive urge to tufts of algae or particles on the bottom, viciously mouthing and ejecting them. Redirected aggression does not fit definitions of displacement activities given by Baerends (1957) and by Tinbergen and van Iersel (1947).

Territorial defense in streams, other than that occurring in reproductive behavior, has been noted for several salmonids including brown trout (Lindroth, 1955, Kalleberg, 1958), Atlantic salmon (Kalleberg, 1958), rainbow trout (Stringer and Hoar, 1955, Newman, 1956), eastern brook trout (Newman, 1956), and coho salmon (Hoar, 1951). Territory is defined as a defended area by Noble (1939), implying aggression against intruders.

Territorial defense was observed in the aquaria and in the stream. Partial territoriality, noted by Greenberg (1947) for the green sunfish, *Lepomis cyanellus*, was also seen in the coho. Defense of the partial territory is the same, toward all but the dominant fish, as that described by other workers for complete territory defense.

Stable hierarchies have been described in stream-dwelling salmonids by Newman (1956) for rainbow and eastern brook trout. Hierarchies have been shown to exist in several other kinds of fishes, such as the green sunfish (Greenberg, 1947), and *Platypoecilus* (Braddock, 1945). Stringer and Hoar (1955) noted no well-organized peck order or nip-right among Kamloops trout.

Fairly stable hierarchies were frequently observed in coho groups within artificial stream channels. When less than 5 fish were present in aquaria, these hierarchies could be ascertained and observed over periods of up to 2 weeks. Hierarchies were usually of the "nip-right" type (Braddock, 1945), in which one fish would nip another without being nipped in return.

The first sign of aggression or agonistic activity in groups of 3 to 5 coho introduced to a channel previously empty of fish usually appeared 5 to 15 minutes after nomads were placed in the observation channel. Initial action was usually a threat. Sometimes the single threat was sufficient to establish a dominance–subordination relationship between a contact pair, especially if the displaying fish was much larger than the object of the threat. The dominated individual usually sank submissively toward the bottom or drifted downstream a short distance.

If the fish placed in the control channel were close to the same size, sometimes the 2 largest fish set up territories, 1 in each pool. Other smaller fish were forced to take up partial territories or shuttle from one territorial fish to another, being nipped or chased upon entering each territory. The area at the extreme head of the upper pool, the "riffle" between pools, and the extreme tail of the channel were areas where subordinate fish usually remained. As long as the subordinates remained close to the bottom out of sight, the dominants paid them little heed. As soon as a subordinate rose to feed, he was nipped or chased. If a co-dominant carried his chase into the other dominant's territory, he was threatened or nipped by the defending territory holder.

Usually, nip-rights rather than territories were established with subordinate fish either shifting position frequently or occupying partial territories. In most observed groups, the first three fish in the nip-right could be easily identified. Relationships among the subordinate fish were usually obscured by the activities of the dominant fish.

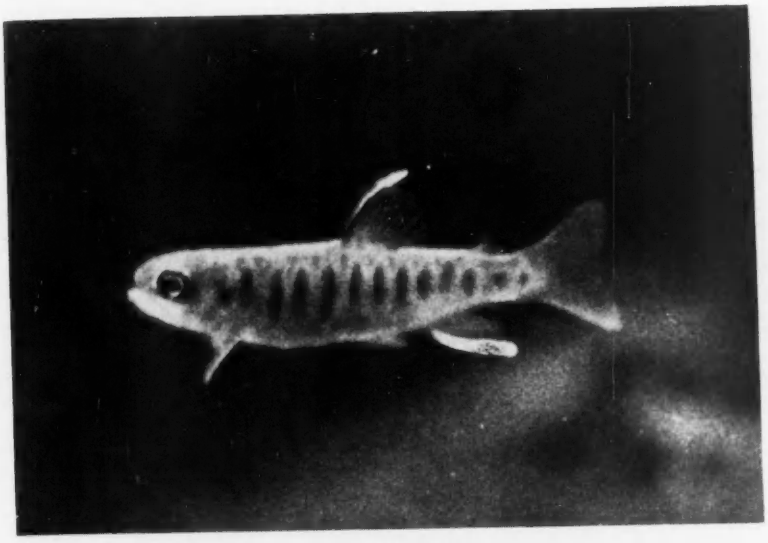

FIG. 9. Lateral threat.

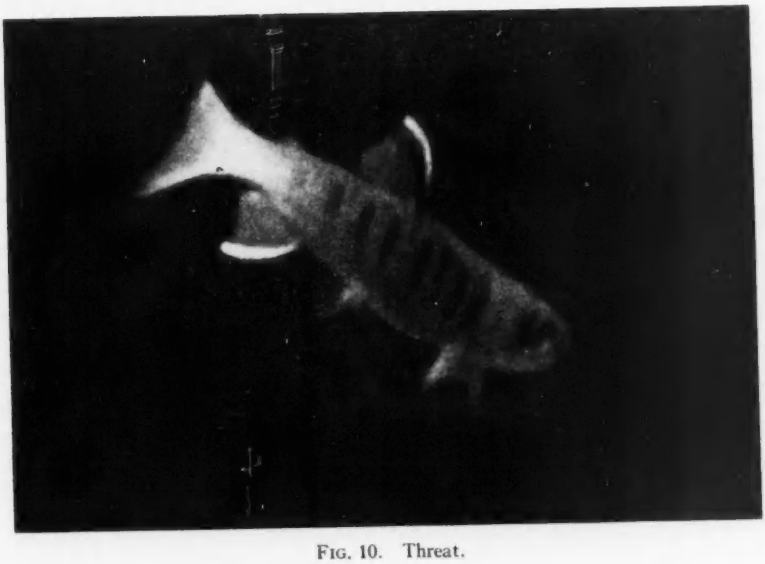

FIG. 10. Threat.

FIG. 11. Nipping.

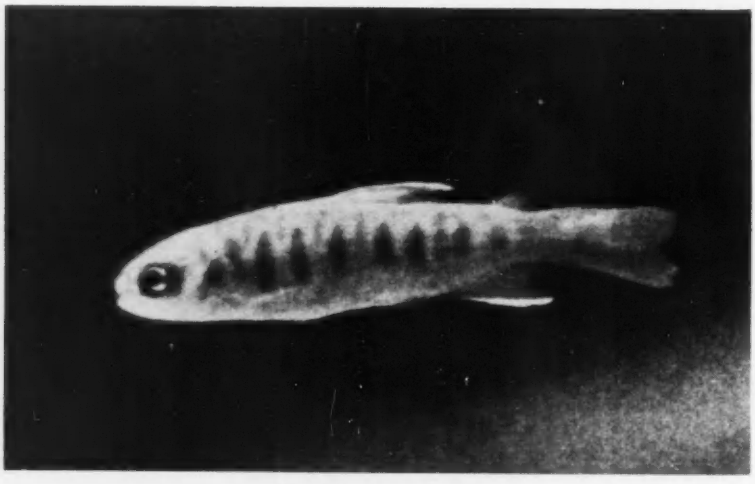

FIG. 12. Submission.

When a group of nomadic coho was added to a channel already containing a resident population, the new fish were usually threatened by the despot in the established hierarchy. If all the new fish were smaller than the despot, they were dominated and forced to submit, either dropping to the bottom or downstream. This domination usually took place in less than an hour.

If some of the new fish were the same size as, or larger than, the residents, a period of up to 4 hours might pass before the resident despot dominated the new fish. But the important observation is that the despot did dominate the introduced fish, even though the latter was larger. Never did a large introduced coho, say 50–60 mm long, dominate the resident despot (45–55 mm). The largest new fish in each introduced group usually passed out of the channel within 24 hours after being dominated by the resident despot. The smaller introduced fish might be dominated by the despot and perhaps by the subordinates, then in a day or two work part way up the hierarchy by dominating resident fish smaller than themselves.

Size was the principal factor governing hierarchy arrangement in all cases observed except as discussed above. Prior residence appeared to govern hierarchy initially, but after a day size again became important.

Often the introduced fish were harassed strongly by the despot and one or more subordinates. On several occasions the submissive introduced fish were seen to be chased out of the trough outlets by aggressive residents.

Noble (1939) points out that in *Xiphophorus*, either a single newcomer if sufficiently large, or a group of new fish, will produce a revolution in the resident hierarchy. In the latter case each fish fights for itself against residents and introduced individuals. While the dominant resident usually remains the despot, a fish from either group may rise to second place in the order. No such rapid revolution was seen in the artificial stream channels, where resident fish held a distinct advantage, but enforced confinement, where fish could not leave the channels, might have eventually produced the "revolution".

Braddock (1949) shows that prior residence in an area confers upon an individual *Platypoecilus* a greater potential for dominance than it would otherwise have. Braddock indicates that this effect is most important in initial contacts between individuals, and that if the intruder is larger than the resident, size may prevail in the contact. Braddock's observations could well be applied to coho salmon, except that the prior resident always prevailed in artificial stream channels. The introduction of intruders larger than the resident despot tended to prolong the conflict between the pair.

Behavior in Artificial Channels at Deer Creek

Capacity of the channels to hold coho was estimated in the period April 15 to May 19, 1960. From 4 to 7 coho, 35–45 mm, were found to remain in the A channels 1 month after introduction. Capacity of the B channels was found to be 3 to 6 coho.

From May 20 to June 16, 1960, 4 experiments were conducted in the B channels to test whether the nomads added to a barren channel would tend to remain there more readily than those added to a resident population. Table I

shows proportions of introduced nomads remaining in the test and control channels. In 3 of the 4 experiments, a greater proportion of the control fish remained.

In 1961 all experiments in A and B channels had as their objective to determine whether nomads would cease movement if adequate living space was provided. From April 21 to May 31, four tests were carried out in the A channels. In all cases a greater proportion of introduced nomads tended to leave the channels where resident coho were already present than left the barren channels.

Flow patterns and bottom configuration in the B channels were altered considerably in 1961. Figure 6 shows the changes made in the bottoms of the channels. Flow was about 6 times greater than it had been in 1960, ranging from 95 to 76 l/min. Five experiments were conducted, and in 4 of these the fish tended to leave the test channel more readily than they did the control channel.

Table I shows details of a sign test (Li, 1957) of the equality of proportions of introduced coho groups remaining in the control and test channels in all suitable experiments in 1960 and 1961. The analysis indicated that the proportion of introduced nomads that remained in the test channels was significantly smaller (at the 1% significance level) than the proportion of nomads remaining in the control channels. In other words, such a difference could have occurred by chance with a probability of 1 in 100.

TABLE I. Test of behavior in A and B channels to determine if nomads added to a resident population had greater tendency to leave their channel than did nomads added to a barren channel. Equal numbers of coho (3 to 5) were placed in each channel at the start of the replication. The test channel had a resident group of coho present.

Replications	Observed proportions remaining		
	Control	Test	Sign of difference
B – May 20–May 27, 1960	1.00	0.60	–
B – May 27–June 1	0.50	0.25	–
B – June 1–June 13	0.50	0.00	–
B – June 13–June 16	0.40	0.40	...
B – Apr. 6–Apr. 21, 1961	0.40	0.60	+
B – Apr. 21–Apr. 24	1.00	0.33	–
B – May 19–May 26	0.66	0.33	–
B – May 26–May 31	0.33	0.00	–
B – May 31–June 10	0.33	0.00	–
A – Apr. 21–Apr. 29	0.66	0.33	–
A – Apr. 29–May 10	0.33	0.00	–
A – May 10–May 19	1.00	0.33	–
A – May 19–May 31	0.33	0.00	–

Number of replications = 12 (omitting B – June 13, 1960).
Hypothetical frequency of negative signs = 6.
$\chi^2 = 8.33$ with 1 d.f. (significant at 1% level).

There appeared to be a tendency for fewer coho to become resident in the test channel in 1961 than had been the case in 1960. The increase in water velocity may have reduced the areas usable as stations and territories. Bottom contours were altered considerably, however, and this may have been responsible for any change in capacity of the channels.

Kalleberg (1958) showed that reduction in water velocity tended to cause territorial Atlantic salmon and brown trout to rise away from contact with the stream bottom and move about the aquarium observation channel. It may be that low-velocity pool environments are more conducive to hierarchy formation than to territoriality, while faster flows elicit greater territoriality. The environments utilized by coho in the study streams are of both slow and fast current types, but the former flow condition is more frequently the case in the period June to October because of low streamflow.

Aggression was less frequent in the control channel than in the test channel during experiments in 1960. Tables II and III show nipping counts in each channel during one experiment.

From June 6 to July 9, both test and control fish were fed daily with brine shrimps to determine if more coho could be held in the troughs by an abundant food supply. When food was introduced each day, all coho usually gorged themselves, then continued to catch and spit out the shrimps. Aggression usually ceased in both channels during feeding, but began again when food ceased to drift downstream.

TABLE II. Nipping in control channel, 12:15–14:15 hours, June 1, 1960. Mean nips given per fish per 10 minutes = 0.25.

	53 mm	46 mm	45 mm	42 mm
Nips given	8	7	0	0
Nips received	0	2	10	3

TABLE III. Nipping in B test channel 12:20–14:20 hours, June 1, 1960.

Lengths of aggressor (*mm*)	Nip recipients (length in *mm*)								
	Residents					Nomads added			
	52[c]	48[c]	41[c]	40[c]	39[c]	53	50	42	40
52	–	0	19[a]	...	2	10	4	8	18
48	0	–	3[a]	...	10	1	3	12	45
41	0	0	–	3	11[b]	0	0	0	8[b]
40	0	0	0	–	...	0	0	0	...
39	0	0	0	0	–	0	0	1	9
53	10	0	0	0	0	–	0	0	0
50	0	0	0	0	0	0	–	1	0
42	0	0	0	0	0	0	0	–	0
40	0	0	0	0	0	0	0	0	–

[a]Some of these nips may have been directed at the resident 40 mm fish. At times the 41 and 40 mm fish could not be distinguished.
[b]Some of these nips may have been made by the resident 40 mm fish.
[c]These resident coho lengths were obtained on June 13, while the nomads were measured on June 1 before they were added to the channel.

Feeding failed to increase the capacity of the troughs to hold coho. Before feeding began, capacity of the channels ranged from 2 to 4 fish one week after introduction of a given group of nomads. After food in excess was supplied, the channel capacities ranged from 1 to 4 fish one week after introduction of a given group of nomads.

Hierarchies were organized in the control channel soon after nomads were introduced. Dominance order in these hierarchies was organized on the basis of size, with the largest coho becoming dominant.

Dominant fish tended to grow more rapidly than subordinate coho. Table IV shows growth of dominant and subordinate fish introduced into the channels at the same time. Growth was determined after the time intervals shown in the table.

TABLE IV. Growth of dominant (D) and subordinate (S) coho in B channels.

Channel and time period		Initial length	Final length	Growth
		mm	*mm*	%
Control channel				
May 11–May 20	D	46	47	2.2
	S	41	41	0.0
	S	39	39	0.0
May 20–June 25	D	43	46	7.0
	S	43	44	2.4
June 1–June 13	D	53	56	5.6
	S	42	44	4.8
June 25–July 1	D	44	46	5.0
	S	42	43	2.5
Test channel				
May 11–June 13	D	45	52	15.0
	S	41	43	5.0
	S	39	41	7.0

From June 16 to July 17, 1960, a series of 3 experiments was conducted to determine if groups of nomads separated by size would react differently in the troughs. Both B channels were cleared of fish and 12 nomads, 39–43 mm, were placed in the control channel and 12 fish, 41–55 mm, were placed in the test channel. Both groups were fed brine shrimps daily. All of the large coho left the test channel within 5 days, but four of the small fish remained in the control channel after 5 days. The largest two of these fish set up territories between which the smaller coho were chased and harassed. One dominant coho occupied the upstream half of the channel while the downstream coho had a partial territory in the lower half of the channel. The latter fish was submissive to the dominant coho, but defended his territory against all subordinates. In the control channel, 26 nips were counted in 25 minutes of observation just after the 12 fish were introduced to the channel. In the test channel, 13 nips were counted in the 45 minutes just after the fish were introduced. Nine days after the start of the experiment, 3 of the small nomads were still in the control channel.

The 2 territorial coho and 1 subordinate remained. Subsequent experiments with groups of coho separated by size indicated that smaller fish would remain in the troughs more readily than larger coho.

From August 18 to September 13, 1960, two experiments were conducted to determine if a group of coho of nearly the same size would exhibit more aggression than a group of fish of disparate lengths. Table V shows nipping frequency in the groups introduced to the channels on August 18. The coho used at this time were resident fish seined from a natural stream area. Aggression was more frequent in the group of coho of near equal size than in the group of disparate size.

TABLE V. Nipping in B channels on August 18, 1960. Fish in right channel were nearly equal in length while those in left channel were disparate in length.

Left channel 60 minutes					Right channel 89 minutes				
Aggressor (*mm*)	58	55	53	51	Aggressor (*mm*)	58	58	58	57
58	–	1	4	4	58	–	7	12	9
55	0	–	0	1	58	3	–	4	6
53	0	3	–	7	58	2	3	–	8
51	0	0	0	–	57	0	0	0	–
Total = 20 nips Nips per 10 minutes = 3.3					Total = 54 nips Nips per 10 minutes = 6.1				

Table VI shows nipping frequency in the groups introduced on September 7. Observations were made periodically from September 7 to 9. Aggression was more frequent among coho of near-equal lengths than among coho of disparate lengths. In both of the experiments from August 18 to September 13, all fish but the dominant coho left the channel.

Behavior in Artificial Channels at Oak Creek

On May 10, 1961, 294 coho fry were taken from the downstream trap at Deer Creek and transported to Oak Creek, near Corvallis. These fish were placed in the artificial channels: 194 in the right channel, 100 in the left. The fry were fed soon after being placed in the channels and daily thereafter. Mean size of the fry on May 10 was 40 mm.

By May 12, 40 fry had moved out of the left channel and 99 had left the right channel. A few fish each week left the channels in the next month. On June 17 all remaining coho were netted from the channels, counted, and measured. Exactly 23 coho were found in each channel. Coho mean lengths were as follows: 49.6 mm in the left channel and 48.6 mm in the right channel. The 1 mm difference between means was not significant at the 5% level.

Calculated density of coho in each channel was 2.9/m² on June 17. In the week before June 17, 10 coho moved out of the right channel and at least 3 departed the left channel. After all coho were counted and measured, they were returned to the channels and the water level was raised 46 cm, so that both

TABLE VI. Nipping in B channels, September 7–9, 1960. Fish in left channel were of similar lengths while those in right channel were disparate in length.

Left channel, 65 minutes					Right channel, 90 minutes				
	Nip recipients					Nip recipients			
Aggressor (*mm*)	62	62	60	59	Aggressor (*mm*)	71	69	65	65
62	–	15	9	4	71	–	0	2	0
62	0	–	0	0	69	1	–	1	0
60	2	0	–	1	65	0	0	–	0
59	0	0	0	–	65	0	0	0	–
Total = 31 nips Nips per 10 minutes = 4.7					Total = 4 nips Nips per 10 minutes = 0.4				

channels were essentially pools. No food was placed in the channels after June 17. No coho left the channels in the following 4 months.

The results of the experiment at Oak Creek indicated that presence of artificial food in excess of the coho daily ration had no apparent influence upon density of fish in the channels. More than twice as much food was placed in the right channel as in the left, yet the coho density was the same in each channel at conclusion of the experiment.

Cessation of all coho movement out of the channels following an increase in water depth, and hence space, suggests that limited living space was the factor causing downstream movement. Other factors may have brought about some of the initial heavy downstream movement following placement of coho in the channels on May 10.

BEHAVIOR IN NATURAL STREAM AREAS

Behavior of resident coho salmon in natural stream areas was observed at several times during the summer and fall of 1960. Table VII shows the results

TABLE VII. Frequency of coho nipping in natural stream areas on Deer Creek, 1960.

Station	Date		Time	Area observed	Mean depth	Bottom	Coho present	Fish per m^2	Nips per fish per 10 min.
	month	*day*	*hours*	m^2	*cm*		*no.*	*no.*	*no.*
–150	8	1	1150–1200	2.3	20	rubble	5	2	0.4
005	8	1	1415–1425	1.5	15	sand	8	5	3.0
040	8	1	1430–1440	3.3	13	gravel	6	2	2.8
120	8	1	1450–1500	1.5	30	silt-sand	5	3	2.4
–125	8	7	1520–1530	1.1	10	silt-sand	6	5	1.7
–125	8	7	1535–1545	1.5	30	rubble	10–12	7	1.5
1100	7	23	1135–1145	2.3	30	silt-sand	12–15	6	3.2
1100	7	23	1200–1210	1.1	15	rubble	5	4	1.8
4250	9	9	0926–0946	1.5	10	gravel	4	3	0.5
3900	9	9	1015–1035	1.5	15	gravel	3	2	0.7
2500	9	9	1045–1055	2.3	25	gravel-silt	5–6	2	2.0
2480	9	9	1105–1125	1.5	10	gravel	4	2	0.4
6500	9	13	1220–1240	1.9	8	gravel	5–6	3	1.6
6180	9	13	1255–1305	2.2	8	gravel-silt	8	3	4.1
2600	9	13	1410–1420	2.2	20	gravel-silt	6–8	3	2.9
3710	9	29	1005–1025	1.5	13	gravel	5	3	1.5
4050	9	29	1045–1105	1.4	33	gravel-silt	3–5	3	0.7
4125	9	29	1110–1120	2.8	13	gravel-silt	11–15	4	2.6

of these observations. Mean density of fish was calculated, and this ranged from 2 to 7 coho per m^2, with a mean of 3. Mean number of nips recorded per fish per 10 minutes was 1.9, ranging from 0.4 to 4.1.

The number of nips relative to depth of water is also of interest. Behavior in water less than 20 cm deep (11 instances) was compared to behavior in water over 20 cm deep (7 instances). No significant difference could be shown between nipping or area occupied per fish in shallow and deep areas.

Observations in natural stream areas were made primarily to estimate the extent of nipping. The most significant point was that nipping was frequent and probably nearly continuous. The comparison of deep and shallow areas to test differences in area and nipping per fish are not regarded as conclusive, since activity in water over about 46 cm deep could not be observed properly.

Figures 13–17 show that downstream-migrant coho became equal in length to residual fish by about November 6 in 1959 and by mid-November in 1960. This period coincided with rise in streamflow due to the first fall rains. Presumably, living space would become more plentiful as water flow increased.

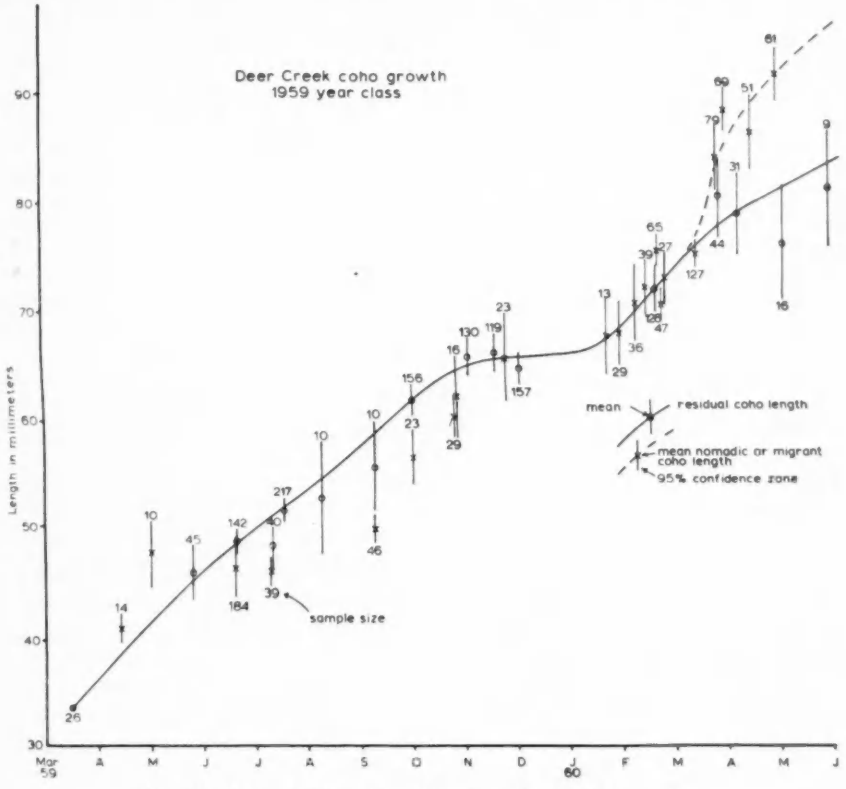

FIG. 13. Growth of juvenile coho in Deer Creek, 1959 year-class

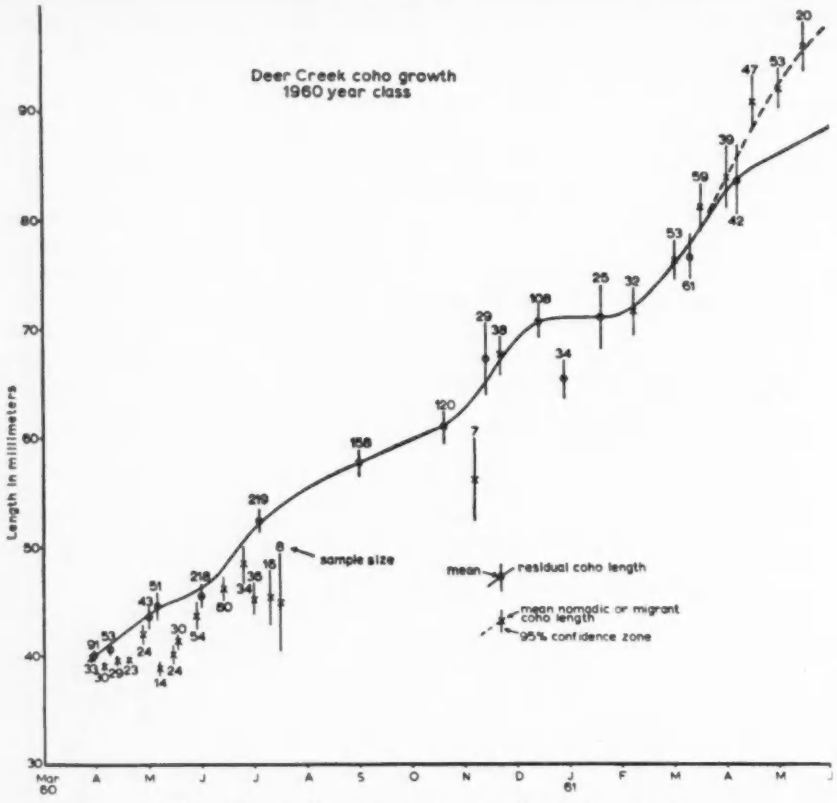

FIG. 14. Growth of juvenile coho in Deer Creek, 1960 year-class.

Early in the winters of 1959 and 1960, the coho salmon changed their place of residence or stations from open, relatively shallow water to deeper pools. They apparently preferred locations with heavy overhead cover. On December 13, 1960, a group of Deer Creek coho was observed with the aid of a water glass. About 10 coho were observed for 20 minutes over a bottom area of about 0.18 m^2. No sign of aggression was noted in this group. All fish held positions close to the bottom, feeding on drifting material. Several fish were only 5 to 8 cm apart. The calculated number of coho per square meter was 54. At the same location on August 1, the fish per unit area had been about 3.2 per m^2 and the nips seen per fish over 10 minutes had averaged 2.4.

On December 20, another group of 7 coho lying close to the bottom in a sheltered area was observed. These fish were congregated over a bottom area of about 0.18 m^2. The density of coho was about 38/m^2 and no nipping was seen in 15 minutes of observation. Three other coho were seen feeding in separate locations about 60 cm apart. No aggression was seen among these fish.

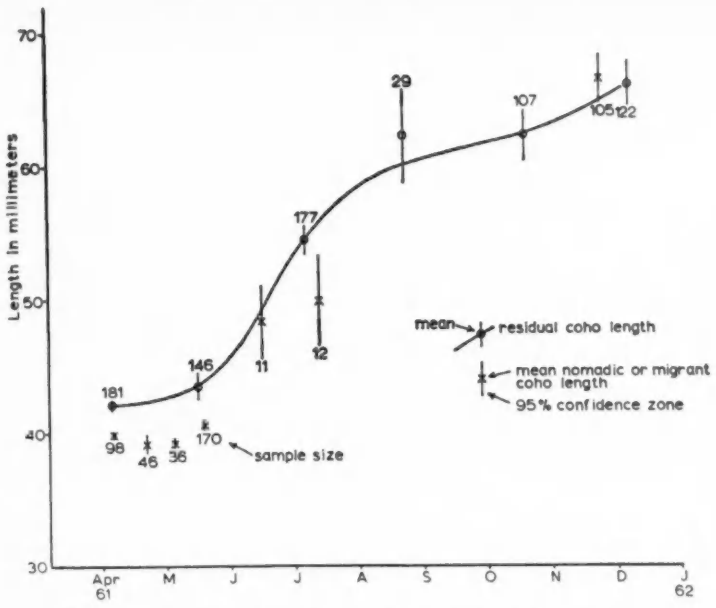

FIG. 15. Growth of juvenile coho in Deer Creek, 1961 year-class.

General observations made during two winters regarding the locations preferred by coho indicated that the young fish preferred deep water to shallow (or preferred slower current), and tended to congregate in areas sheltered by overhead cover. Coho smolt aggregation noted by Hoar (1951) was associated with a preference for cover. Cover and slow current preferences may well have caused the aggregation of coho observed in the study streams. However, a lessening of aggressive behavior must have occurred, for the dense groupings seen in the streams were never observed in the spring, summer and fall months (of the first year of life) when aggressive behavior was a frequent occurrence.

The tendency of coho to aggregate, or a lessening of aggressive behavior, could have been responsible for the cessation of downstream movement of fry smaller than residual fish in early winter.

BEHAVIOR IN CONTROLLED STREAM SECTION

On July 13, 1960, the 39 m^2 controlled stream section was electro-sampled and 34 coho were removed. Mean fork length of these fish was 53 mm. Beginning July 13, nomads from the Deer Creek downstream trap were placed in the uppermost pool of the section as follows: July 13, 55 mm; July 14, 39 and 40 mm; July 17, 42 and 43 mm; July 20, 45 and 47 mm; July 23, 42 mm; July 25, 53 and 55 mm; July 31, 41 and 57 mm; August 31, 41 mm.

All nomads were marked by removal of one ventral fin. The absence of a resident coho stock when nomads were introduced and the presence of a trap

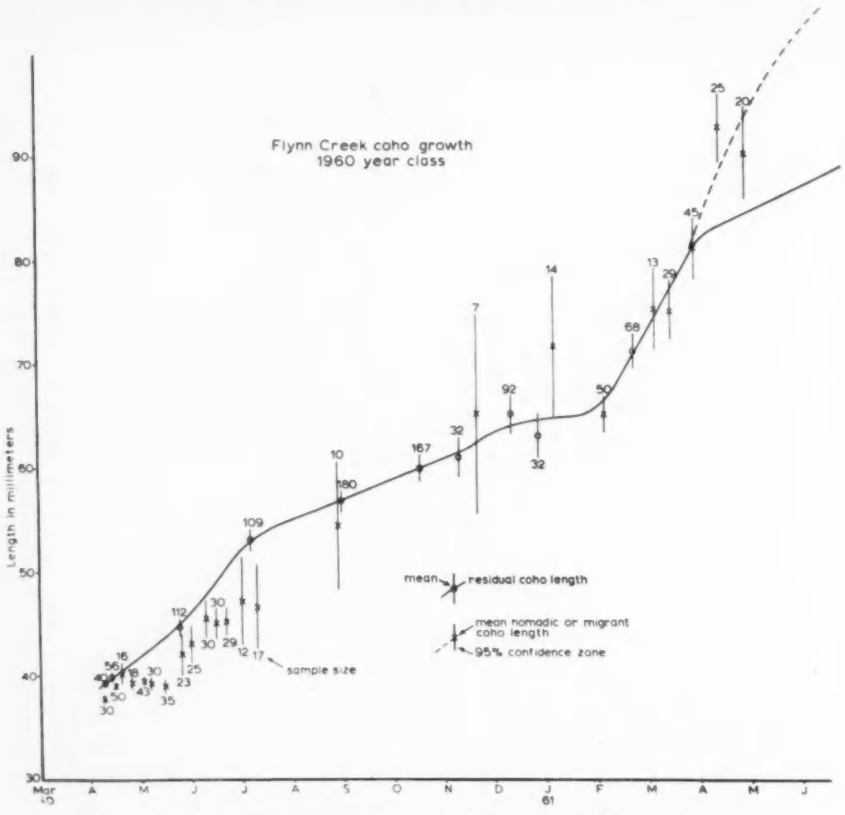

FIG. 16. Growth of juvenile coho in Flynn Creek, 1960 year-class.

at the outlet and a barrier screen at the upper end of the section were the principal ways in which this section differed from an uncontrolled section.

On September 7, 1960, the section was electro-sampled to remove all coho. Eight marked fish were found, out of 12 introduced coho that should have been present; their lengths were 63, 61, 59, 57, 54, 52, 47 and 40 mm. The 4 fish not found could have been shocked but lost under debris, could have suffered mortality in the section, or could have moved out of the section during two brief periods of possible leakage.

All the marked fish recovered were found in the pool where they were released, in spite of the fact that two pools were available below the uppermost one (Fig. 8). This probably indicated that population density never became sufficiently high in the upper pool to cause fish to move into lower pools. If all 12 introduced nomads had remained in the upper pool, coho density there would have been only about 1 fish per m^2, less than half the mean density shown in Table VII. During the test period, 3 cutthroat trout, 93 to 122 mm, and

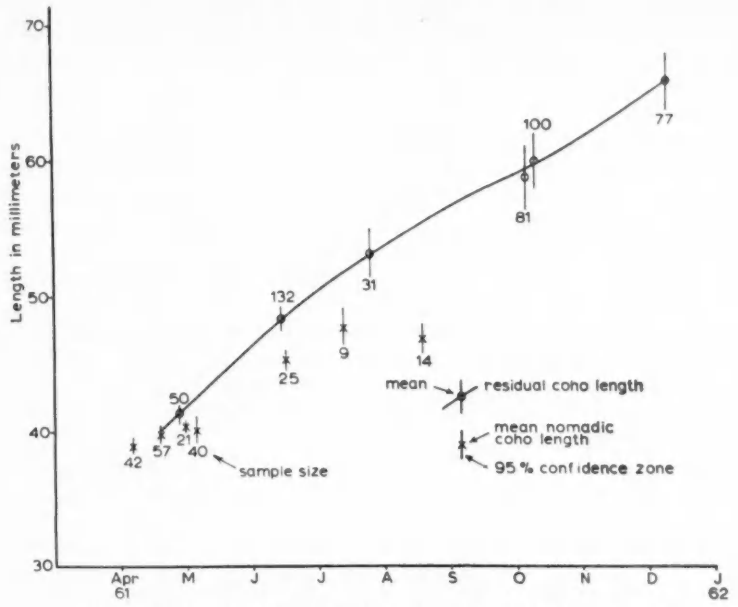

FIG. 17. Growth of juvenile coho in Flynn Creek, 1961 year-class.

one 77-mm cottid were taken in the outlet trap, indicating that the trap would catch and hold fish moving downstream. Mesh of the trap was sufficiently fine to hold the coho fry if they had moved.

TRANSFER OF FRY TO AREA BARREN OF RESIDENT STOCK

Of the 1627 nomads transferred from Flynn Creek to Needle Branch from April 16 to May 6, 1960, about 4% moved through the downstream trap in the 1 month following their transfer. It should be noted that the stream was barren of naturally-spawned coho fry at time of the transfer.

Of the 1577 nomads transferred from Flynn Creek to Needle Branch from April 19 to May 4, 1961, about 27% moved through the downstream trap in the 1 month following their transfer. Naturally recruited fry were present in Needle Branch when the Flynn Creek nomads were released in Needle Branch. These results again indicated that introduced nomads would tend to remain in a stream area barren of resident stock, and tend to leave if resident stock were present.

GROWTH AND MOVEMENT OF NOMADS

Observations of dominance–subordination relationships in artificial stream channels indicated that slight differences in length of individual fish in contact pairs were sufficient to bring about subordination of smaller fish. Differences as slight as 1 mm were found to be important. For this reason, the "growth" curves for nomadic and residual coho of the same year class should be examined carefully.

Figures 13, 14 and 15 show "growth" curves for nomadic and residual coho of the 1959, 1960 and 1961 year classes on Deer Creek, and Figures 16 and 17 show the same information for the 1960 and 1961 year classes on Flynn Creek. Table VIII for the 1959–1961 year classes shows the results of comparisons of mean lengths of residual and nomadic coho. Pairs of samples considered were taken at the same time. In all pairs of samples on Deer and Flynn Creeks (these included all available data taken at suitably similar times) taken from shortly after emergence in spring to early fall, the nomadic coho were smaller in mean length (P values 0.10 to 0.01). These differences are all the more remarkable in that samples of residual fish almost certainly included some coho

TABLE VIII. Comparisons of mean lengths (L) of residual and nomadic or migrant coho, year-classes 1959–1961, in Deer and Flynn Creeks. The last column, P, is the upper limit of the range in which the significance level of the length difference lies.

Nomads or migrants			Residuals			Diff. in length	t	Max. P
Date	No.	L	Date	No.	L			
		mm			*mm*	*mm*		
Deer Creek—**1959** *year-class*								
Jun 15–20/59	184	47.42	Jun 18/59	142	48.80	1.38	1.95	0.10
Jul 8–10/59	39	46.07	Jul 8/59	40	48.25	2.18	1.92	0.10
Jun 15–Jul 10/59	223	47.18	Jun 18–Jul 8/59	182	48.68	1.50	2.45	0.02
Sep 8/59	46	50.00	Sep 8/59	10	56.00	6.00	3.03	0.01
Oct 26/59	16	62.44	Nov 3/59	130	66.11	3.67	1.84	0.10
Mar 26/60	81	85.02	Mar 28/60	44	80.84	4.18	1.77	0.10
Apr 15/60	54	87.89	Apr 8/60	31	79.35	8.54	3.47	0.01
May 1/60	67	93.93	May 4/60	16	76.69	17.24	6.11	0.01
Flynn Creek—**1959** *year-class*								
Apr 1/60	54	87.11	Mar 17–Apr 4/60	8	77.00	10.11	3.04	0.01
Apr 15/60	41	89.32	Apr 11/60	7	81.28	8.04	1.75	0.10
Deer Creek—**1960** *year-class*								
Apr 4/60	30	39.17	Mar 28/60	91	40.15	0.98	3.34	0.01
Apr 26/60	24	42.08	Apr 30/60	43	43.65	1.57	2.18	0.05
May 6/60	14	38.86	May 4/60	51	44.73	5.89	8.39	0.01
May 24–31/60	54	43.89	May 30/60	218	45.66	1.77	2.10	0.05
Jul 5–11/60	16	45.50	Jul 3/60	219	52.59	7.09	5.49	0.01
Nov 21/60	38	67.81	Nov 14/60	29	67.38	−0.43	−0.23	0.90
Flynn Creek—**1960** *year-class*								
Apr 8/60	30	37.87	Apr 9/60	40	39.30	1.43	4.72	0.01
Apr 14/60	15	38.47	Apr 13/60	56	39.95	1.48	2.69	0.01
May 23/60	23	42.17	May 23/60	112	44.68	2.51	2.37	0.02
Jul 3–14/60	17	46.71	Jul 6–8/60	109	53.10	6.39	3.16	0.01
Deer Creek—**1961** *year-class*								
Apr 4–8/61	98	39.79	Apr 4–6/61	181	42.05	2.26	8.07	0.01
May 16–19/61	170	40.68	May 16/61	146	43.54	2.86	6.35	0.01
Jul 7–14/61	12	50.00	Jul 5/61	177	54.56	4.56	2.75	0.01
Nov 23–27/61	105	66.60	Dtc 7/61	122	66.15	−0.45	−0.36	0.80
Flynn Creek—**1961** *year-class*								
Apr 28–29/61	21	40.52	Apr 27/61	50	41.34	0.82	1.78	0.10
Jun 16/61	25	45.44	Jun 14/61	132	48.52	3.08	4.89	0.01
Aug 18/61	14	46.93	Jul 25/61	31	53.32	6.39	6.08	0.01

that would soon become nomadic. If these fish could somehow have been removed from the residual samples, the disparity between nomads and residuals would have been greater. As the available data show, at some time in the fall the coho moving downstream become equal in mean size to residuals. In early spring the migrants become larger than the residual fish.

Needle Branch data were not used because of artificiality in growth data introduced by transfer of Flynn Creek nomads.

Earlier in this paper it was pointed out that random movement might explain the downstream drift of coho fry. If this were so, there should have been a rather considerable upstream movement of fry. Huntsman (1945) reported movements of Atlantic salmon parr downstream and upstream.

Table IX shows the catch of downstream and upstream traps during periods when juvenile upstream traps were operated. Obviously there is very little movement upstream of fry, and the nomads passing downstream apparently do not return upstream to any important extent.

TABLE IX. Monthly distribution of coho fry movement at traps.

Trap	Period	Downstream	Upstream
Needle Branch	May, 1960	128	No trapping
	June	52	1
	July	8	3
	August	12	7
	September	0	1
	October	8	0
Needle Branch	April, 1961	249	1
	May	368	0
	June	27	0
	July	10	3
	August	1	5
	September	3	1
	October	0	1
Deer Creek	September, 1960	0	0
	June, 1961	123	0
	July	22	6
	August	4	0
	September	4	0
	October	4	0
Flynn Creek	June, 1961	171	No trapping
	July	23	1
	August	23	Trap defective
	September	4	0

DISCUSSION

Study of coho behavior in artificial stream channels and natural stream areas has demonstrated that aggressive behavior among coho is frequent, in fact nearly continuous in the period from emergence of fry until fall. Experiments conducted in artificial stream channels, in a controlled-stream section, and in a natural stream show that nomadic coho will tend to cease downstream movement if offered an environment with sufficient space free of resident coho.

Nomadic coho are smaller on the average than coho that do not move downstream. Size governs position in social hierarchies and outcome of contacts between coho, with larger coho having the advantage.

The foregoing facts indicate that aggressive behavior is one factor causing the spring downstream movement of coho fry. It appears probable that this factor, perhaps in combination with other density–regulatory factors, would tend to cause the density of resident coho per unit area to remain rather constant each year. If this is the case, then the yield of coho migrants, or smolts, should not fluctuate very greatly from year to year, although streamflow differences might cause some fluctuations.

Since data on yearly coho smolt yield from Deer Creek, Flynn Creek and Needle Branch are incomplete, data obtained by others should be reviewed. Hunter (1959) shows total numbers of coho smolts leaving Hooknose Creek on King Island, British Columbia, from 1948 through 1957 (Table X).

TABLE X. Hooknose Creek coho migrations, 1948–1957, Data from Hunter (1959) and unpublished records of the Fisheries Research Board of Canada.

Smolt migration year	Smolt numbers	Females in parent run	Sibling fry migration
1948	7,959	...	...
1949	3,550	221	2100
1950	2,982	198	22031
1951	4,389	277	20512
1952	3,620	71	8155
1953	4,034	29	5062
1954	5,987	228	29417
1955	6,756	72	15767
1956	4,508	162	7779
1957	6,074	229	32220

The number of smolts in a given year bears no evident relationship to the number of adult females in the parent run or to the drift of sibling fry. In the same time interval, the total number of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon fry, *O. keta*, passing out of Hooknose Creek, ranged from 98,524 to 1,409,225 (Hunter, 1959), with great fluctuations from year to year, particularly in the case of pink salmon. Of course, these species leave fresh water soon after emerging from the spawning gravel. The 1-year period of residence undergone in Hooknose Creek by the coho appears to be a stabilizing influence upon the number of smolts.

Salo and Bayliff (1958) show data from Washington for Minter Creek smolt migrations for several years. Data shown in Table XI are for those years when no hatchery-reared fish were placed in the stream above Minter Creek trap. Footnotes indicate that age 2/ coho are included in some of the smolt counts and not in the others. In spite of the uncertainty resulting from this, it appears that the total number of wild smolts migrating from Minter Creek does not fluctuate greatly from year to year.

TABLE XI. Minter Creek coho downstream fry and smolt migrations, 1938–1949. Data on fry movement from unpublished data of the Washington Department of Fisheries.

Smolt brood	Females in parent run	Sibling fry	Smolts (1+)
1938	967	52,000	35,452[a,b]
1940	1,393	211,136	32,085[c]
1942	786	60,000	31,893[b]
1943	906	?	23,117[b,d]
1944	500	101,000	30,408[b,d]
1946	500	24,614	41,848[d]
1949	114	920	27,691[d]

[a]Includes some 2+ fish of 1937 brood released after hatchery rearing.
[b]Number of age 2+ fish of this brood not known.
[c]Includes 6829 age 2+ wild fish and some age 2+ fish of hatchery origin.
[d]Includes some wild age 2+ fish of previous brood year, number unknown.

Two other research facilities have been used to secure coho data over the past several years. One of these is a weir on Gnat Creek, tributary to the lower Columbia, operated by the Oregon Fish Commission. Data from this station are not available for reference. A trap on Spring Creek, tributary to the Wilson River near Tillamook, Oregon, was operated by the Oregon Fish Commission from December, 1949 to August, 1958. Some data secured there (Oregon Fish Commission, 1958) are shown in Table XII.

TABLE XII. Spring Creek coho migrations, 1948–1952.

Adult brood year	Females passed upstream	Resulting juveniles	
		Fry out	Smolts out
1948	11[a]	1701	1055
1949	24[a]	1594	1228
1950	35	2498	1947
1951	54	9377	1209
1952	12	4662	1887

[a]These figures may be minimal due to high water.

Broods after 1952 were affected by passage of controlled numbers of females, and are not considered here. The smolt migration in the years of record tended to be relatively constant.

Data on downstream movement of 0/ age coho are available for Minter, Spring, and Hooknose creeks. Data secured at Hooknose Creek, Table X, indicate that a large movement of 0/ age coho does occur there. Mode of the movement generally occurred in late April or May in the 12 years of record. Operation of the Hooknose Creek weir ceased in early June in most years, hence no data are available for the summer movement, if any, of 0/ age coho.

Gnat Creek coho fry movements apparently are similar in timing to those on other streams for which data are available. Three peaks in yearly juvenile downstream movement are known (Oregon Fish Commission, verbal communication): in spring (age 0/), November (age 0/), and the following spring (age 1/).

Spring Creek coho fry movements occur largely in spring, and their magnitude in the years of record (Table XII) bears no particular relationship to the parent runs or to the sibling smolt migrations.

Minter Creek data shown in Table XIII (unpublished data of Washington Department of Fisheries), suggest that fry movement is related to parent egg potential, but some of these same data, Table XI, show that the smolt migration bears no relationship to parent egg potential or sibling fry movement. All fry moving downstream into the Minter Creek trap were placed back upstream. Examination of Salo and Bayliff's (1958) tables, their appendix, and the data of our Table XIII, indicates that a relatively greater total fresh water mortality occurs in years of large egg deposition and large fry migration.

TABLE XIII. Minter Creek coho fry movement downstream, 1937–1957, and parent egg potential.

Brood year	Parent egg potential	Fry movement
1937	?	23,000
1938	?	52,000
1939	none	none
1940	4,577,398	211,130
1941	none	none
1942	1,873,038	60,000
1943	2,092,860	?
1944	1,376,500	101,000
1945	none	none
1946	1,097,000	24,614
1947	none	none
1948	186,200	805
1949	287,864	920
1950	none	none
1951	1,086,684	86,800
1952	1,929,186	105,000
1953	1,150,413	34,672
1954	812,500	32,334
1955	396,000	821
1956	603,000	4,374
1957	650,000	8,319

All available evidence indicates that the year of stream residence undergone by coho tends to stabilize the fluctuations caused by varying parent egg potential, producing a smolt yield of relatively uniform magnitude from year to year, in a given stream.

Smoker (1953) examined coho salmon yield to the commercial fishery in the Puget Sound area in relation to total stream runoff in year of stream residence for given year-classes. He obtained a strong positive correlation. The two most logical effects of greater streamflow upon coho production would be in increasing the effective spawning areas for adults and in providing greater living space for juveniles.

Neave (1949) shows a lower availability of coho to sportsmen fishing Cowichan Bay, B.C., for year-classes which experienced low summer flows in their juvenile stages in the Cowichan River. McKernan *et al.* (1950) show a significant correlation between annual coho salmon catches in Oregon near the

Siletz River and summer low flows of that river 2 years previously. A similar test on data from the Coquille River area showed no significance. Wickett (1951) shows 2 low counts of coho leaving Nile Creek, B.C., associated with 2 years of low summer rainfall in a 4-year interval from 1946 to 1949.

The results of these investigations tend to show that yield of smolt cohoes is positively correlated with summer streamflows, but they do not define the mechanism involved, be it associated with predation, disease, territoriality, food supply, or combinations of these.

As mentioned earlier, downstream drift of coho fry could be due to one or more of the following factors (in addition to aggression in the fry population): displacement by current, innate tendency to migrate, or random shifts in position. The latter possibility has already been shown to be unlikely.

Displacement by current is an attractive explanation for fry movement since this would explain the disparity in size of residual and nomadic fry, the latter being smaller and perhaps less able to hold position in the current. However, as Fig. 13–17 show, the size differences are slight, and should not be sufficient in themselves to explain nomad movement, particularly when some of the fry that move are larger than some of the fry that remain in the stream. Furthermore, current speeds decrease from April through June while mean size of fish increases, making inability to hold in the current an unlikely possibility.

It is likely that a part of the spring downstream emigration of coho fry, probably the portion of the movement that occurs soon after emergence of fry, is due to current displacement or to an innate migration urge, for a few fry (from the first emerging groups of coho) are known to move downstream soon after emergence. This drift occurs in spite of the apparent abundance of quiet marginal water area for living space. The very early arrivals at the downstream traps are 37–39 mm in length.

Hoar (1953) points out that coho fry actively defend territories during the day, then settle to the bottom and become inactive at night, a behavior characteristic that leads to permanent residence in the stream. This type of settling behavior was noted in artificial stream channels and in natural stream areas as well. In both areas, fry tended to be on or close to the stream bottom in hours of darkness. Feeding activity commenced in artificial channels with the first increase in light level at dawn.

Settling behavior at night is not conducive to displacement by current. Activity at night, on the other hand, would be conducive to displacement, as Hoar (1953) indicates. Figure 18 illustrates preference of coho fry for night movement. Data were obtained by Deer Creek trap checks at dawn, dusk, midnight and noon. This preference was marked in March and April, less so in May. Activity at night or a failure to settle and hold close to the bottom evidently leads to nomad movement.

The work summarized in this paper indicates that downstream movement would cease if the drifting fish were placed in a suitable environment free of a resident population of coho. This, in turn, suggests that failure to hold position, either in daylight or at night, is due largely to the presence of other fish. If

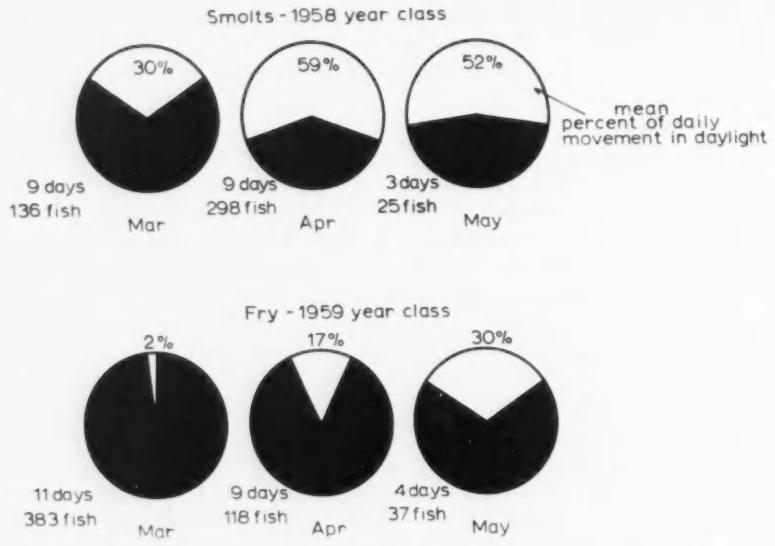

FIG. 18. Downstream movement of juvenile coho in Deer Creek during daylight and darkness, 1959.

fry are forced by aggression into locations unsuited for settling and holding, displacement by current should play a part in causing downstream drift.

Kalleberg (1958) states that territoriality in Atlantic salmon and brown trout is a characteristic evolved as a food supply mechanism. This also is a logical explanation for the aggressiveness of coho, a fish which depends strongly upon drift food on the surface and in the mid-water. However, a similar Darwinian explanation could be offered involving pathological organisms and predation. Aggressiveness could act as a population spreader, decreasing probability of disease, parasite-caused mortality, or predation.

Allee (1938) and Collias (1944) present evidence that a dominant position within a group is correlated with greater individual survival potential. Noble (1939) reported that dominant individuals in a group of *Xiphophorus* sp. lost less weight during periods of starvation than did subordinates, that larger and heavier fishes occupied positions of greater dominance, and that prior residence was an advantage in contacts with newcomers. Braddock (1949) reported similar results for *Platypoecilus* sp.

Aggression seems to be sufficient to account for part of the considerable range in size of cohoes at a given time. As indicated by artificial stream studies reported here, growth of dominant fishes is greater than that of subordinates. Some of the variability in size stems from varying emergence times and varying sizes at emergence of fish emerging at the same time. The rather remote possibility of a feedback mechanism of growth control also exists (Rose, 1960). Brown (1957) suggests that growth of small *Salmo trutta* may be inhibited by the

mere presence of larger individuals or by increased production of adrenocorticotropin due to stress (stress being caused by the presence of larger individuals).

It is suggested that aggressiveness of coho is one factor tending to stabilize numbers of smolts yielded by unit areas, operating as a population spreader. The spread of coho populations after emergence, as streamflow decreases and growth proceeds, should assure adequate food supply for the aggressive members of the population, may help reduce transmittal of pathological organisms, and should insure better survival of aggressive coho. These aggressive fish should have better growth opportunity and pass out of the predation-vulnerable small size classes most rapidly.

At first glance, one might find an anomaly in the explanation of aggression as a food supply mechanism and the fact that experimental provision of excess food did not decrease aggression or alter capacity of artificial stream channels for coho. However, it is probable that aggression is a relatively inflexible innate characteristic that can be little altered by temporary changes in food availability.

Another anomaly appears to exist in the fact that some nomads are larger than many residual coho, and should therefore have been able to dominate smaller fish and obtain adequate living space. However, space for a 40-mm coho may not be adequate for a 50-mm fish, nor do the areas occupied by various size groups appear to be similar in physical characteristics. Then, too, some of the movement of large nomads may be due to an innate "desire" to migrate.

The selective advantages gained by coho through aggression are obvious. Probably there is a limit maximizing profitable aggression at a level compatible with maximum growth and survival. Further extension of fish beyond this maximum should result in over-expenditure of energy for maintenance at the expense of growth (Ivlev, 1945) and hence survival probability (Ricker and Foerster, 1948).

Theoretically, a coho stream rich in drift food should have a native race of coho with smaller territorial requirements than would be the case in streams with low food availability. That such differences in food grade exist is almost certain. The environmental differences found in the range of coho salmon are very great (Shapovalov and Taft, 1954; Salo and Bayliff, 1958; Neave, 1949), and should be sufficient to cause large differences among streams in quantity of seston.

As pointed out earlier, the mechanism whereby increased water area yields more coho has not been isolated. The most likely possibilities, entirely apart from spawning area considerations and confined to living space, are decreases in disease and parasite-caused mortality, decreased predation, increased food supply, or increased area for territory-holding fish. It is probable that all these factors play a part in increasing coho smolt yield. It is suggested that the intense and continuous aggressive activity of coho plays an important role in survival.

SUMMARY

1. A study of aggression in coho salmon was conducted from March, 1959 to October, 1961, in three small Oregon streams. The principal objective of the

study was to determine if emigration of coho fry, occurring from time of fry emergence to November of the first year of life, was caused by aggression in the coho population.

2. The study was made in artificial stream channels and natural stream areas. Glass-sided observation channels were used for part of the study.

3. Downstream movement of coho fry began soon after fry emergence in spring. A large movement took place in the late spring and lesser numbers of nomads moved downstream through the summer and fall. Upstream movement of fry was negligible.

4. Coho fry moving downstream from spring to early fall (these fry are called "nomads" here) were smaller than residual coho. From March to June, migrant smolts were larger than residual yearling coho.

5. Coho behavior patterns and phenomena noted repeatedly in artificial stream channel aquaria included lateral display, parallel swimming, threat, nipping, chasing, flight, hiding, fighting, submission, territorial defense, redirected aggression, and formation of hierarchies.

6. Nomads placed in artificial stream channels barren of fish formed hierarchies and tended to remain in the channels rather than migrating downstream through the unscreened channel outlets.

7. Nomads added to existing resident groups of coho in artificial channels were dominated by the resident dominant fish and tended to leave the channels.

8. Hierarchies and territories observed in artificial stream channels were organized on the basis of fish size, with smaller fish either leaving the channels or being continuously harassed. Small fish that remained in the channels were chased and nipped unless they remained still near the stream bottom or hid among bottom particles, either of the latter two situations resulting in inferior opportunities for feeding and growth.

9. Dominant coho grew more rapidly than subordinate fish in artificial channels.

10. Feeding of coho with brine shrimps, in quantities in excess of requirements, did not alter capacity of artificial stream channels for nomads.

11. Aggression observed in natural stream areas was frequent, probably continuous, and consisted of territoriality, partial territoriality, nipping, threatening, and chasing.

12. Nomads transferred to a 39 m^2 controlled stream section barren of other coho remained there, taking up residence in the pool where they were released.

13. Of 1627 nomads taken from one stream in 1960 and transferred to another stream barren of resident stock, about 4% moved down and out of the stream in 1 month following their transfer. Of 1577 nomads transferred in like manner in 1961, but added to an existing population, about 27% moved down and out of the stream in the month following transfer.

14. It was concluded that aggressive behavior is one factor causing the downstream movement of coho fry.

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The Free Fatty Acids of Cod Oil
1. Anomalous Composition by Fatty Acid Chain Length[1]

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ABSTRACT

Discrepancies have been noted in the relative proportions of certain fatty acid components of the free fatty acids of cod oil, compared to the composition of the neutral fraction. These have been studied quantitatively through gas–liquid chromatographic chain-length analyses of the hydrogenated methyl esters of the fractions. It is suggested that specific enzyme and bacterial actions may be responsible.

Examination of the fatty acid composition of a Newfoundland cod oil by gas–liquid chromatography during the course of other investigations (Ackman *et al.*, 1962a) indicated that the proportion of docosahexaenoic acid, relative to docosenoic acid, was much lower in the free fatty acids (FFA) than in the neutral lipids. The proportion of eicosapentaenoic acid, relative to eicosenoic acid, did not show as great a discrepancy. In the C_{20} and C_{22} fatty acid groups of fresh cod liver oil the monounsaturated and polyunsaturated fatty acids mentioned above are virtually the sole components and are present in roughly equal proportions in each group (Ackman *et al.*, 1962b). The proportion of myristic acid in the cod oil was significantly higher in the FFA, but the other component fatty acids did not show such extreme changes. Three other cod oils from other sources were then examined and the same general conclusions could be drawn.

These gas–liquid chromatograms were obtained on polyester substrates, where the order of appearance of the methyl ester peaks homogeneous in carbon chain length, but differing in degree of unsaturation, is in order of increasing degree of unsaturation. It is therefore probable that overlapping will occur between a less saturated ester peak of one chain length and a more highly unsaturated ester peak of a shorter chain length. While the docosahexaenoate peak is probably free from such interference, the possibility exists with the other three long-chain acid esters in question. In order to avoid quantitative errors of this type the materials were hydrogenated on a semi-micro scale and the relative proportions by chain lengths only were compared (Table I). The chain length analyses are in broad agreement with the general analyses.

A further advantage of working with the saturated materials obtained by hydrogenation is that accurate response factors have been developed for the methyl esters of the longer chain saturated fatty acids (Horrocks *et al.*, 1961). These were checked with the gas–liquid chromatographic apparatus employed

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TABLE I. Percentage fatty acid chain length composition (w/w) and properties of various cod oils, of the neutral and acid fractions, and of fresh cod liver oil (CLO).

	Newfoundland						Nova Scotia						
Oil Source:	Southeast coast			Northeast coast			Sambro Harbour (April)			Terence Bay (April)			Terence Bay (January)
Percentage FFA:	10.8			11.0			27.9			23.5			0.2
Iodine value* of methyl esters:	169.5	172.3	154.0	155.4	156.1	139.2	144.3	143.0	147.5	145.2	144.3	152.1	178.4
Fraction:	Whole	Neut.	FFA	Whole	Neut.	FFA	Whole	Neut.	FFA	Whole	Neut.	FFA	Fresh CLO
Chain length	%	%	%	%	%	%	%	%	%	%	%	%	%
C_{14}	4.2	4.0	5.5	5.4	4.8	6.1	4.4	4.3	5.4	3.6	3.6	4.3	3.7
C_{16}	22.7	22.4	27.6	26.1	24.4	31.2	20.7	21.6	21.3	20.8	20.0	20.7	21.9
C_{18}	28.0	27.4	31.0	26.0	26.9	28.6	27.6	25.7	29.8	27.9	26.9	30.7	28.2
C_{20}	24.2	23.2	21.6	23.8	24.1	20.8	24.4	23.4	24.0	24.4	24.9	24.8	23.1
C_{22}	20.0	22.4	13.2	18.0	18.3	11.9	21.7	23.6	17.8	21.8	23.2	18.6	21.2
Other**	0.9	0.6	1.1	0.7	1.5	1.4	1.4	1.7	1.7	1.5	1.4	1.1	1.9

*By hydrogenation.
**Chiefly C_{18} and C_{17} in roughly equal proportions.

in these studies against a standard mixture of known composition and the factors of Horrocks *et al.* were found to be applicable when analyses of the methyl esters of saturated fatty acids were carried out on both non-polar (SE-30 silicone) and polar (diethylene glycol succinate (DEGS) or butanediol succinate (BDS)) substrates. The data in Table I therefore represent the absolute percentage composition by weight of the methyl esters in question. No corresponding response factors have been reported for the highly unsaturated fatty acids characteristic of marine oils and their proportions are not presented in the present study.

The reduction in the proportion of docosahexaneoic acid is apparent not only in the reduced proportion of the C_{22} group FFA determined in the Newfoundland cod oils (Table I), but also in the lower iodine value of the FFA fraction. In these oils there is also a reduction in the C_{20} group FFA, presumably due to some loss of eicosapentaenoic acid. In the Nova Scotia oils, possibly due to the higher FFA content, these changes are less marked.

A further difference in the oils from the two sources lies in the relative increases in the FFA of the proportion of the C_{16} and C_{18} group fatty acids, representative in the one case of roughly equal quantities of hexadecanoic and hexadecenoic acids, and in the other of almost exclusively octadecenoic acids. In the Newfoundland oils the greater increase takes place in the C_{16} group, while in the Nova Scotia oils it is in the C_{18} group and little change is observed in the C_{16} group. The relative iodine values also reverse themselves in the Nova Scotia oils, but this cannot be obviously correlated with the changes in the C_{18} or C_{22} groups of fatty acids.

While the highly unsaturated acids in question are very susceptible to air oxidation, this should affect equally the docosahexaenoic and eicosapentaenoic acids, hence any specificity may be ascribed to enzyme action. Under the conditions employed in "sun-rotting" cod livers it is to be expected that bacteria

present will produce lipolytic enzymes in addition to the enzyme systems normally present in cod livers (Drummond and Hilditch, 1930; Brocklesby, 1941; Guttmann and Vandenheuvel, 1958). The influence of the contents of the bile sac cannot be entirely discounted, and the question of the extended storage of the Newfoundland oils must also be considered.

The discrepancies in the docosahexaenoic and myristic acid compositions of the FFA make it difficult to suggest a single mechanism accounting for both changes, since one is negative and the other positive from the proportion point of view, yet interconversion seems unlikely. In general lipolysis seems to be independent of fatty acid chain length (C_{12}–C_{18}) and degree (0–2 double bonds) of unsaturation (Kates, 1960). Preferential hydrolysis at specific ester linkages in the triglyceride molecule, considered in relation to the now accepted view that fatty acid distribution in glycerides is not random (Youngs, 1961), offers the most reasonable explanation.

EXPERIMENTAL

Materials

Industrial cod oils were supplied through the courtesy of Fishery Products, Ltd., St. John's, Newfoundland. Two lots were obtained, one each from the northeast coast and the southeast coast. These represent blendings of various lots of oil of relatively low FFA content. The further samples were obtained directly from the rotting barrels in Nova Scotia, one from Terence Bay and one from Sambro Harbour. The FFA content was determined (as oleic acid) by the procedure given in the Official and Tentative Methods of the American Oil Chemists' Society, revised to 1961.

Separation of FFA

Cod oil (500 g) was dissolved in high-boiling petroleum ether (Iosol 1520, 500 ml). This was shaken with 1:1 methanol–water mixture (1000 ml) containing 5% excess KOH over that necessary to neutralize the FFA. The soap phase was washed with two batches of Iosol (100 ml each) and the Iosol phase with two batches of water (100 ml each). The washings were combined with the respective phases. Iosol (200 ml) was added to the soap phase, and both fractions were acidified with HCl (3*N*) and washed until neutral. A small portion of emulsified and semi-solid matter, chiefly from the soap phase, was discarded, but total recoveries were 95–98%. A nitrogen atmosphere was maintained in this and all other procedures dealing with unsaturated materials.

Preparation of Methyl Esters

Whole cod oil and some samples of neutral fraction were saponified and the fatty acids recovered, while other samples of neutral fraction were transesterified with methanol. Large-scale esterifications of acids were carried out in methanol with HCl catalyst but small-scale esterifications were carried out variously with the same system, with methanolic BF_3, or with diazomethane. No significant difference existed in gas–liquid chromatograms of methyl esters prepared by different procedures from the same materials (cf. Vorbeck *et al.*, 1961).

Hydrogenation

Samples of methyl esters (50–100 mg) were hydrogenated in a precision semi-micro hydrogenation apparatus (Vandenheuvel, 1952). Complete hydrogenation was assured since close duplication of hydrogen values was obtained with various size samples. Gas–liquid chromatograms of different hydrogenated lots of the same material were comparable within experimental error.

Gas–liquid Chromatography

The apparatus employed was a Wilkins "Aerograph". Columns were copper tubing 10 feet in length and $\frac{1}{4}$ inch in diameter, packed with 25% substrate on 60–80 mesh Chromosorb. The operating temperatures were 220 or 230° and helium at input pressures of 30 or 20 psi was the carrier gas. A "Disc" integrator was employed for peak area determinations. Analyses of unsaturated esters were carried out on DEGS substrate, and of hydrogenated esters on SE-30 or BDS, the latter giving somewhat less tailing, although results were comparable. Application of the correction factors of Horrocks *et al.*, 1961 reduced the average deviation on mixtures of saturated acids of known composition[2] (calculated as % w/w) from the order of 4.7 to 1.7, with a slight remaining tendency to negative bias as the fatty acid chain length increased.

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The Relative Efficiency of Nylon and Cotton Gill Nets for Taking Lake Trout in Lake Superior[1]

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ABSTRACT

The change from cotton to nylon twine for gill nets in 1949–52 resulted in a sharp increase in the efficiency of the most important gear used for taking lake trout in Lake Superior, and, consequently, biased estimates of fishing intensity and abundance severely.

From early May to the end of September 1961, short gangs (2000 or 4000 linear feet) of cotton and nylon nets were fished in parallel sets for lake trout. A total of 343,000 feet of gill netting was lifted. Nylon nets were 2.25 times as efficient as cotton nets for taking legal-sized fish and 2.8 times as efficient for undersized lake trout. The average lengths of legal, undersized, and all lake trout taken in nets of the two materials did not differ greatly. The percentage of the catch which was undersized (less than 1.25 lb, dressed weight) was 20.8 in nylon nets and 17.7 in cotton. The relative efficiency of cotton and nylon nets showed no trend during the season. The efficiency ratio determined in this study was closely similar to that obtained by earlier workers.

Correction of estimates of fishing intensity and abundance for the greater efficiency of the nylon nets used since 1951 has not been attempted. The drastic decline of the lake trout fishery has forced fishermen to make changes in fishing practices in the past few years that cause new bias of an unknown extent to estimates of fishing intensity.

INTRODUCTION

The modern gill-net fishery in the upper Great Lakes differs greatly from the early fishery. The early gill nets were made of relatively coarse twine, had crude wooden floats, and were lifted by hand into open rowboats or sailboats. A long progression of improvements in equipment and methods has occurred since then. Power boats (first steam, then gas and diesel), enclosed and heated and with hulls capable of breaking through ice, have increased the length of season and the range of operation. Power lifters increased the amount of gear that could be handled, so that some fishermen lift as much as 10 miles (16 km) of net in a day; and recently fathometers and automatic pilots have assisted in location of suitable grounds and have reduced the need for manpower. The improved equipment enables fishermen to find their net buoys in fog or snow as far as 60 miles (96 km) from shore with uncanny ability.

Changes in the gill nets themselves have also been great. The structure and preparation of wooden floats were improved, and since 1925 aluminum floats have eliminated any depth limitation on fishing.[2] Increases in the efficiency of gill-net twine have kept pace with other improvements. Twine became finer

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[2]Nets are commonly fished in Lake Superior at depths down to 120 fathoms (220 m) and have been set in at least 150 fathoms (275 m). Usually few fish are taken below 120 fathoms.

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and more pliable and two changes in basic material have taken place. During the 1930's the softer, more elastic cotton thread replaced linen in most major fisheries and in the late 1940's and early 1950's nylon twine in turn replaced cotton. The shift from cotton to nylon twine brought about the greatest single increase in the efficiency of gill nets that has occurred. The earlier change from linen to cotton did raise efficiency (we lack the quantitative data on the matter), but that increase was small compared to the one resulting from the later change from cotton to nylon.

The conversion from cotton to nylon twine in the large-mesh gill nets of Lake Superior[3] took place over the period 1949–52 — principally in 1950 and 1951. A change of gear at this time was peculiarly inopportune for the administrators and scientists who needed to follow the lake trout (*Salvelinus namaycush*) fishery by analysis of statistics on effort and catch per unit of effort. The recent collapse of the lake trout fisheries of Lake Huron (Hile, 1949) and Lake Michigan (Hile *et al.*, 1951a) had created a strong market demand for Lake Superior lake trout and had provided great incentive for increased fishing effort. At the same time, the population of sea lampreys (*Petromyzon marinus*) in Lake Superior was expanding and its effects were soon to be felt (Hile *et al.*, 1951b). Then, at the beginning of a period of drastic decline in the fishery, the efficiency of the major fishing gear, the large-mesh gill net, was suddenly increased sharply. Fishing intensity, as computed from the amount of gear lifted, was henceforth greatly underestimated; and availability or abundance, based on catch per unit of effort, was to the same degree overestimated.

Extensive observations on the fishery were badly needed during the shift from nylon to cotton twine, but the Bureau was without the staff to make them. The only observations possible were those of Leo F. Erkkila[4] on a small number of lifts off Marquette, Michigan, in 1950. His findings, mentioned briefly by Hile *et al.*, (1951b), indicated that nylon gill nets took about 2½ times as many lake trout as linen nets fished in the same gang.

The states were not asked to require fishermen to record the kind of gill-net twine on their monthly fishing reports during the period of change. It would have been highly indiscreet to solicit this information at a time when pressures existed for legal restrictions on the use of nylon twine. Study of changes in the catch per unit effort of other, trout-producing gears, to judge the increase in efficiency of gill nets after nylon twine came into use, was unproductive (Hile, 1953). In spite of the known higher efficiency of nylon twine, the ratio of the catch per unit effort of set hooks to gill nets changed little with the conversion — suggesting that set hooks and gill nets exploited segments of the lake trout stock that were to some degree independent.

Estimates of fishing intensity and availability have, therefore, been based on greatly biased data since 1949. The Bureau was in position only to warn as

[3]This paper applies specifically to gear and methods used in United States waters of Lake Superior, but the fishery in Canadian waters is very similar.

[4]At that time Fishery Research Biologist in charge of the Bureau of Commercial Fisheries field station at Marquette, Michigan, and now Assistant Director, Sea Lamprey Control, of the Bureau's Biological Laboratory in Ann Arbor, Michigan.

to the direction of the bias and term it severe. The first opportunity to make a systematic study of the relative efficiency of cotton and nylon gill nets for taking lake trout in Lake Superior came in 1961. The present paper is a report on the results of that inquiry.

MATERIALS AND METHODS

Arrangements were made to have a commercial operator conduct the experimental fishing under supervision near Huron Bay (south-central Lake Superior). He was paid for fishing the cotton nets along with his own nylon nets.

New cotton nets totaling 9400 feet (2870 m) were made up for the experiment. Of this total, 5400 feet (1650 m) had a mesh of $4\frac{9}{16}$ inches (115.9 mm) and 60/6 twine, and 4000 feet (1220 m) had a mesh of $4\frac{5}{8}$ inches (117.5 mm) and 70/6 twine. The use of two sizes of mesh and twine was unavoidable — they were all that were readily available. Both sizes of mesh and twine were commonly used in 1946–49, however. The heavier 60/6 twine was fished most frequently in Wisconsin and the 70/6 twine in Michigan.[5] The nylon nets were of $4\frac{5}{8}$-inch mesh and 46/4 twine, the most common combination in use at the present time (1961). The cotton nets were hung on the one-half basis as was customary when they were the standard gear, and the nylon nets were hung on the five-eighth basis (8 feet of netting, flat mesh, on 5 feet of maitre) as is common now.

The cotton nets were fished in short gangs, usually 2000 or 4000 feet long (610–1220 m), set in a straight line approximately at right angles to the contours of the banks and roughly parallel to several similar gangs of nylon nets. Nets were left in the lake for 3 to 7 nights between lifts. In the spring when the water was very cold, they were usually left out 6 or 7 nights, but in late summer they could be left for only 3 nights. The fishing was done from early May through the end of September. All sets were made within the depth range of 8-38 fathoms (15-70 m). Whenever a gang of cotton nets was lifted, it was replaced by a gang of nylon nets regardless of the catch. The cotton nets were usually moved to another location along the same bank where they replaced a gang of nylon nets. After the middle of June, not all of the cotton nets could be fished simultaneously. They had to be reeled and dried periodically. Because of this periodic removal, and because there were more nylon gangs than cotton, it was not possible to alternate cotton and nylon gangs for all lifts. Catches were not consistently good or poor at any single location along the bank. It is believed that the system of replacing cotton gangs with nylon every lift (usually resetting the cotton gangs in place of nylon) made the data from the two gears closely comparable.

All lake trout caught in cotton nets and in nylon nets were measured (total length, to longest tip of the tail) and the total catches of legal-sized fish in each were weighed to the nearest $\frac{1}{2}$ pound (227 grams), dressed weight (viscera and

[5]In Michigan, some fishermen believed that finer cotton twine more than paid for the cost of more frequent replacement and used 80/6, 90/6, and even 100/6 thread in their nets. The nets used in this experiment cannot, therefore, be considered typical of the entire fishery in either Wisconsin or Michigan.

gills removed). Under the conditions of fishing it was impractical to keep separate records for the two kinds of cotton nets. To all appearances the catches were approximately the same.

EARLIER COMPARISONS OF NYLON AND COTTON GILL NETS

Past studies of the comparative efficiency of nylon and cotton or linen twine have been based on several species and have yielded a variety of results (Table I). Molin (1950, 1951) reported on parallel fishing with nylon and cotton twine in Swedish lakes. Nylon twine caught between 2 and 3 times as much of several species, including whitefish (*Coregonus* sp.) and burbot (*Lota lota*), as cotton. No trout were caught. Molin (1953) made another series of experiments with cotton, spun nylon, and monofilament nylon. The poundage of whitefish in spun nylon was 1.7 times that in cotton. Monofilament nylon has not yet been used in the Great Lakes. Lawler (1950) found that nylon nets

TABLE I. Summary of past observations on the relative efficiency of nylon and cotton gill nets. The "efficiency ratio" is the catch of the nylon nets divided by the catch of the cotton nets.

Author	Lake	Species	Efficiency ratio	
			By weight	By number
Atton (1955)	La Ronge Last Mountain	Lake trout	*ca.* 2	...
Hewson (1951)	Winnipeg	Sauger, walleye, burbot	3	...
Lawler (1950)	Erie	Whitefish	3.2	...
Molin (1950)	Mälar	Principally roach[a]	...	3
Molin (1951)	Mälaren	Perch[b] and roach[a]	2	...
	Siljan	Whitefish[c]	*ca.* 3	...
	Bruntträsket	Burbot	*ca.* 2	...
Molin (1953)	Storavan	Principally whitefish[c]	1.7	...

[a]Presumably *Rutilus rutilus*.
[b]*Perca fluviatilis*.
[c]*Coregonus*, species not given.

were 3.2 times as efficient as linen nets fished in the same gang for whitefish (*Coregonus clupeaformis*) in Lake Erie. Hewson (1951) showed that nylon twine of 3-inch mesh was 3 times as efficient for sauger (*Stizostedion canadense*), walleye (*S. vitreum vitreum*), and burbot as cotton in Lake Winnipeg. Atton (1955) found that nylon nets of 5-inch mesh were about twice as efficient as cotton nets of the same mesh for lake trout in Lac la Ronge and Last Mountain Lake. Kennedy (1956), however, could find no evidence from the fishery statistics of Great Slave Lake that nylon nets of 5½-inch mesh were more efficient than cotton nets of the same mesh size for either whitefish or lake trout. His conclusions were based on comparisons of two groups of fishermen operating in the same general

area; one fished principally nylon nets and the other principally cotton nets. The two groups did not, however, use the same techniques of fishing. Consequently the Kennedy statement is not recorded in Table I.

Most studies, then, have indicated advantages for nylon over cotton ranging from a little less than two times to slightly more than three times. The one exception, just described, was not based on experimentation.

Atton (1955), Molin (1951, 1953), and Hewson (1951) all reported that the fish taken in nylon nets were somewhat larger than those taken in cotton nets. Kennedy (1956) mentioned that fishermen in Great Slave Lake generally believed that nylon nets take smaller fish than do cotton nets, but could find no evidence to support this belief.

Several commercial fishermen on Lake Superior suggested that the time of year the two materials were fished would affect their relative efficiency. Others suggested that if both were fished in the same gang, lake trout might lead along the cotton nets and be caught in the nylon. Most studies have not covered a sufficiently great time span to test the first suggestion, but the agreement between the findings of Lawler (1950) and Erkkila and those of other workers suggests that no great bias is introduced by fishing nets of both materials in the same gang.

CATCHES OF LEGAL AND UNDERSIZED LAKE TROUT IN NYLON AND COTTON GILL NETS

Most of the monthly records of take were based on substantial lifts of both kinds of gill nets. The amount of gear lifted ranged from 18,000 feet (5500 m) in July to 32,300 feet (9900 m) in May for cotton, and from 32,000 feet (9800 m) in July to 50,000 feet (15,300 m) in August for nylon (Table II). The catch per

TABLE II. Amount of cotton and nylon gill nets lifted, pounds of legal-sized (1¼ lb dressed) lake trout caught, catch per unit effort, and comparative efficiency of nylon and cotton twine. (10,000 feet = 3050 m)

Month (1961)	Number of feet of net lifted		Pounds of legal-sized lake trout caught				Efficiency ratio
			Total		Per 10,000 feet of net		
	Cotton	Nylon	Cotton	Nylon	Cotton	Nylon	
May	32,300	40,800	94.0	250.0	29.1	61.3	2.1
June	22,000	41,800	45.5	249.5	20.7	59.7	2.9
July	18,000	32,000	34.0	114.0	19.1	35.5	1.9
August	30,000	50,000	107.5	424.5	35.8	84.9	2.4
September	32,000	44,000	111.0	330.0	34.7	75.0	2.2
Total	134,300	208,600	392.0	1,368.0	29.2[a]	65.6[a]	2.25[b]

[a]Based on grand totals.

[b]The unweighted mean of the monthly values was 2.30.

10,000 linear feet of net lifted ranged from 19.1 lb in July to 35.8 lb in August for the cotton nets and from 35.5 lb in July to 84.9 lb in August for the nylon nets (28.4–53.2 kg/10,000 m in July, 52.8–126.3 in August). Although the quality of the fishing varied considerably from month to month, no trend was apparent in the comparative efficiency of the two materials. Nylon nets caught from 1.9 to 2.9 times the poundage of legal-sized lake trout taken by cotton nets per unit effort in different months, but the variation of the ratio was random. The most valid figure for the comparative efficiency is probably the ratio of the catches per unit effort in nylon and cotton nets as determined from the combined poundages for the 5-month period. For this period the catch per unit effort of legal-sized lake trout in nylon nets was 2.25 times that of the cotton nets. The unweighted mean of the monthly efficiency ratios (2.30) had almost the same value. A figure of $2\frac{1}{4}$, then, constitutes a sound estimate of the ratio. This value is only slightly below the figure of $2\frac{1}{2}$ determined by Erkkila for nylon nets fished in the same gang with linen nets. Apparently, leading of fish along the linen nets to the nylon nets in the same gang did not materially influence the catch in nylon gear. Cotton twine probably is slightly more efficient than linen twine.

The relative efficiency of nylon and cotton for catching undersized lake trout is of some interest because the regulations of all administrative agencies on Lake Superior specify minimum sizes for lake trout as well as minimum mesh sizes for gill nets. The number of undersized trout caught varied greatly from month to month, but the comparative efficiency of the two materials again showed no consistent trend (Table III). For the 5-month period, nylon nets averaged 7.8 trout of sub-legal size per 10,000 feet (3050 m) of net lifted, and cotton nets

TABLE III. Number of undersized lake trout caught in each month and number taken per unit effort in nylon and cotton nets. (10,000 feet = 3050 m)

Month	Number of undersized trout				Efficiency ratio (by numbers of fish)
	Total		Per 10,000 feet		
	Nylon nets	Cotton nets	Nylon nets	Cotton nets	
May	27	6	6.6	1.9	3.5
June	58	12	13.9	5.5	2.5
July	30	11	9.4	6.1	1.5
August	20	3	4.0	1.0	4.0
September	27	3	6.1	0.9	6.8
Total	162	37	7.8[a]	2.8[a]	2.8[b]

[a]Based on grand totals.

[b]Because of the small numbers of fish taken in cotton nets in some months, presentation of the unweighted mean of the ratios is not desirable.

averaged 2.8. Nylon nets were, therefore, about 2.8 times as efficient for undersized trout as cotton nets, as compared with 2.25 times for legal-sized trout. Since the undersized trout were not weighed, it was not possible to calculate the comparative efficiency of nylon and cotton for all sizes of fish in terms of poundage.

SIZE OF LAKE TROUT CAUGHT IN NYLON AND COTTON GEAR

As was mentioned in a previous section, most comparisons of nylon and cotton nets have shown the average size of fish taken in nylon nets to be larger than that of fish caught in cotton nets. This study failed to indicate such a relation. The average weight of legal-sized trout (greater than 1.25 lb or 0.57 kg, dressed) taken in nylon nets did not differ significantly (was 0.03 lb less) from that of fish taken in cotton nets (Table IV). Although the total number of fish taken in cotton nets was small, the mean weight of individual legal trout taken in cotton gear was the greater in 4 of the 5 months. The one exception occurred in the month of smallest total catch.

TABLE IV. Average dressed weight, in pounds, of legal-sized lake trout (1¼ lb dressed, or larger) taken in nylon and cotton nets, May–September, 1961. (1 lb = 454 g).

Month	Nylon nets	Cotton nets	Difference
May	2.03	2.19	0.16
June	1.96	1.98	0.02
July	2.03	1.72	−0.31
August	2.43	2.44	0.01
September	2.44	2.52	0.08
Average	2.22	2.25	0.03

Among lake trout of all sizes (both legal and undersized) the cotton nets took longer fish (average length 19.2 inches or 487 mm) than did nylon nets (18.9 inches, 480 mm) — see Table V. The differences between the two gears in the mean length of fish of legal or below legal size were slight, but the nylon nets were relatively the more effective in the entanglement of smaller lake trout in the range 14.0 to 17.9 inches (354–455 mm) — (Fig. 1). Cotton nets were relatively more effective for fish in the range 20.0 to 20.9 inches (508–531 mm). The percentage of undersized lake trout in the catch of nylon nets was 20.8 as compared with 17.7% in cotton nets. These figures give support to the evidence of the previous section on the relatively greater ability of nylon nets to take undersized trout (efficiency ratio, favoring nylon, of 2.8 for undersized fish compared to 2.25 for legal-sized lake trout). Nylon twine's greater selectivity for lake trout several inches shorter than the modal frequency is a reflection of its greater capacity for entangling various head and body parts rather than its ability to hold gilled fish of that size. Few, if any, lake trout less than 18 inches

TABLE V. Total-length distributions, average lengths, and percentage undersized, for lake trout taken in nylon and cotton nets (1 inch = 2.54 cm).

Length interval (*inches*)	Nylon nets		Cotton nets	
	Number of fish	Percentage	Number of fish	Percentage
6.0– 6.9	1	0.1	...	...
7.0– 7.9	...	...	...	...
8.0– 8.9	...	...	1	0.5
9.0– 9.9	2	0.3	...	...
10.0–10.9	...	...	...	...
11.0–11.9	1	0.1	...	...
12.0–12.9	3	0.4	3	1.4
13.0–13.9	10	1.3	3	1.4
14.0–14.9	14	1.8	3	1.4
15.0–15.9	66	8.5	12	5.7
16.0–16.9	70	9.0	15	7.2
17.0–17.9	96	12.3	17	8.1
18.0–18.9	107	13.8	31	14.8
19.0–19.9	135	17.3	33	15.8
20.0–20.9	122	15.7	48	23.1
21.0–21.9	81	10.4	23	11.0
22.0–22.9	34	4.4	10	4.8
23.0–23.9	23	3.0	4	1.9
24.0–24.9	7	0.9	3	1.4
25.0–25.9	4	0.5	2	1.0
26.0–26.9	1	0.1	1	0.5
27.0–27.9	...	...	...	...
28.0–28.9	1	0.1	...	...
Total	778	100.0	209	100.0
Average length				
Legal	19.8	...	20.1	...
Undersized	15.4	...	15.2	...
All fish	18.9	...	19.2	...
Percentage Undersized	...	20.8	...	17.7

(457 mm) long have a great enough girth to be held in nets of mesh $4\frac{5}{8}$ inches (118 mm), but they are caught by the teeth, head bones, or fins.

Atton (1955) showed that the principal difference between the selectivities of nylon and cotton nets was that nylon nets took a greater proportion of fish from the upper end of the size range taken by both materials. Selectivity on the lower end of the size range was nearly identical for the two twines. This observation applied to catches of ciscoes (*Leucichthys* sp.), whitefish, and walleyes taken in nets of 1.5, 2 and 5 inches mesh (38, 51 and 127 mm). Almost exactly the opposite appears to be true for lake trout. The difference in selectivity is principally in the 6- or 7-inch interval immediately below the modal frequencies — not at either end of the range. The number of fish longer than 22 inches (559 mm) is so small that evaluation of net selectivity for the larger lake trout is not possible. The slightly higher percentage representation of lake trout greater than 24 inches (610 mm) long in cotton nets must be considered insignificant.

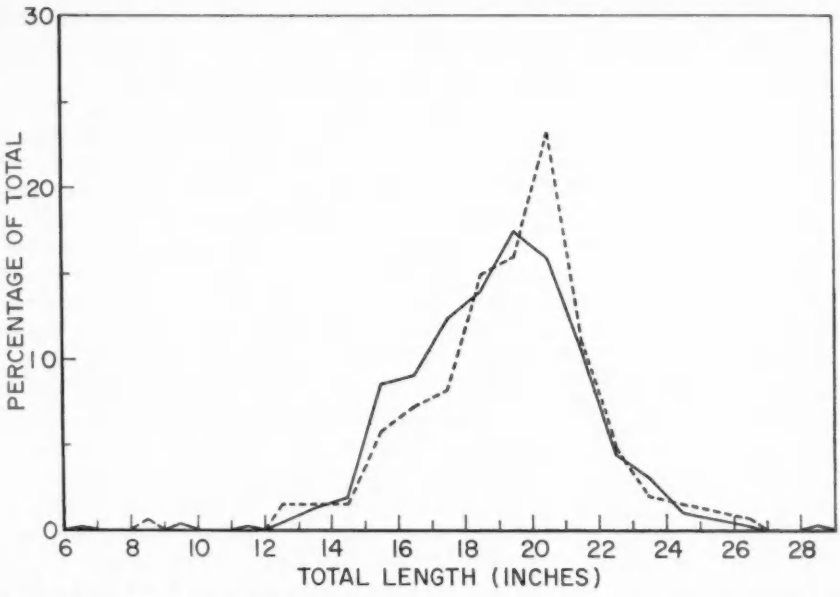

FIG. 1. Percentage length distribution of lake trout caught in nylon and cotton gill nets. *Solid line*, nylon nets; *broken line*, cotton nets.

In former years, before sea lamprey depredations drastically reduced the numbers of larger lake trout, fish up to 30 inches (762 mm) long were common in the catches of nets of $4\frac{5}{8}$-inch (118 mm) mesh, and the proportion of fish 22 to 30 inches (558–762 mm) fish was much greater than it is now. In late summer and fall, concentrations of large trout were great enough that nets of mesh $5\frac{1}{2}$ and $6\frac{1}{2}$ inches (140 and 165 mm) were commonly fished. Obviously, the percentage of undersized fish was considerably lower in the former fishery.

INTERPRETATION OF RECENT LAKE TROUT STATISTICS

The close agreement between our finding that nylon gill nets are 2.25 times as efficient as cotton nets for taking legal-sized lake trout in Lake Superior and Erkkila's earlier observation of a 2.5-fold advantage of nylon over linen twine, gives evidence that both studies yielded reasonably dependable results. The general agreement of the Lake Superior studies with those of other investigators lends additional support to this view. It would seem then that the value 2.25 for the efficiency ratio could be used to "correct" the records of fishing effort for gill nets beginning in 1951 (when nylon had almost completely replaced other twine). This correction would automatically adjust the catch per unit effort for gill nets and thus shift the indices of both fishing intensity and abundance to levels fairly comparable to those for years prior to use of nylon nets.

The correction of gill-net records might well be valid for the early 1950's, but since then other biasing influences have developed. A trend began toward concentration of fishing effort on the better grounds in the best seasons. The poorer fishermen were forced to cease operations altogether and the better fishermen turned to fishing other species during slack periods. This trend continued steadily until, by 1959, the lake trout fishery was a part-time operation limited to the winter and spring months for all but a few fishermen. In 1960 and 1961 only one fisherman on the entire United States shore of Lake Superior fished for lake trout steadily through all the summer and fall months. Abundance indices calculated from an annual average catch per unit effort on a full-time fishery are not comparable with those from the present part-time fishery. Therefore, even though we can now feel confidence in a value for the efficiency ratio of nylon and cotton gill nets fished for lake trout, correction of recent lake trout statistics still would yield undependable figures. The changes in the fishery have been great and further changes are to be anticipated as sea lamprey control and lake trout rehabilitation continue in the years immediately ahead.

When lake trout stocks have again attained some measure of stability the fishery may well become re-established under conditions considerably different from those prevailing in former years. For example — either the total catch or total fishing effort may be controlled; commercial sport trolling may increase to a point where it takes a significant part of the total catch; minimum mesh sizes, size limits, and season closures may be altered. After the fishery is re-established, a new base period of reference should be established to follow fluctuations.

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The Enzymic Digestion of Cod Tropomyosin[1]

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ABSTRACT

Tropomyosin from cod muscle can be oxidized with performic acid to cleave disulphide bonds without degradation of other amino acid residues. The ε-amino groups of lysine within the molecule can be substituted readily with carbobenzoxy-groups for protection against digestion by trypsin. The digestions by trypsin of carbobenzoxy-substituted tropomyosin, and by chymotrypsin of oxidized tropomyosin, have been shown to be reproducible, providing peptides suitable for amino acid sequence studies. The peptides so obtained were separated by ion-exchange chromatography using a Beckman/Spinco Amino Acid Analyzer.

After treatment with urea, cod tropomyosin does not yield a free N-terminal amino acid as has been reported for rabbit tropomyosin.

INTRODUCTION

Tropomyosin, a protein first isolated from rabbit skeletal muscle by Bailey (1946, 1948) and subsequently demonstrated to be present in muscle of many different species, has a rather unusual amino acid composition (Bailey, 1948; Yoshimura, 1955; Kominz *et al.*, 1957; Kubo, 1957; Saad *et al.*, 1959; Hoogland *et al.*, 1961). The role played by this protein, which contains a large number of polar groups in the molecule, is still obscure. Since the successful elucidation of the structure of insulin by Sanger and Tuppy (1951, 1951a) and Sanger and Thompson (1953, 1953a), efforts have been made to correlate protein structure with biological activity. Tropomyosin would appear to lend itself to a similar approach: it can be obtained in quantity in a relatively pure form and can be highly purified if necessary; it is an extremely stable protein which does not denature readily (Bailey, 1948). The amino acid composition encourages the study of their sequential arrangement: the absence of tryptophan allows oxidation with performic acid for the cleavage of disulphide bonds without destruction of an amino acid residue, and provides an easy check of the purity of the protein preparation; the presence of certain amino acid residues in small numbers, e.g. proline, phenylalanine, cystine, histidine, tyrosine, and glycine could provide valuable clues to the sequential order of overlapping peptides obtained by different methods of hydrolysis of the protein. However, tropomyosin does possess a most undesirable feature, that of size, since it contains an estimated 455 amino acid residues per molecule (Hoogland *et al.*, 1961). The largest protein molecule of which the amino acid sequence has been determined, the protein subunit of tobacco mosaic virus (Tsugita *et al.*, 1960), contains 158

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amino acid residues. Light and Smith (1960, 1960a), and Light *et al.* (1960), have reported the sequence of amino acids of some peptides obtained from papain which contains 185 residues. As Anfinsen (1958) has pointed out, proteins containing a large number of amino acid residues present "the general problem of the specific hydrolysis of a protein molecule to yield reproducible fragments of moderate size".

In this laboratory, several enzymes have been investigated for their ability to produce "reproducible fragments of moderate size" from cod tropomyosin, both substituted and native. This paper reports the results of the enzyme hydrolyses which seem to fulfil this requirement, that is, the action of trypsin on carbobenzoxy-substituted tropomyosin, and the action of chymotrypsin on oxidized tropomyosin.

After this work has been completed, Saad and Kominz (1961) reported that glutamic acid had been found to be the N-terminal amino acid of rabbit tropomyosin. Previously, no N-terminal amino acid had been found for this protein (Bailey, 1951; Kubo, 1957; Chibnall and Spahr, 1958). The method of Saad and Kominz (1961) for the analysis of N-terminal acids was applied to the tropomyosin obtained from the Atlantic cod (*Gadus callarias*) that was used in these studies. The results are included in this paper.

MATERIALS

TROPOMYOSIN. A bulk preparation was made from the fillets of fresh Atlantic cod (*Gadus callarias*) according to the procedure of Dingle and Odense (1959) with modifications for large-scale preparation as suggested by Hoogland *et al.* (1961). The purity of the tropomyosin was checked by tryptophan analysis and moving-boundary electrophoresis as described by the same authors.

TRYPSIN. Obtained as a twice-crystallized (50% $MgSO_4$) preparation from Worthington Biochemical Corporation, Freehold, New Jersey.

α-CHYMOTRYPSIN. Obtained as a crystalline salt-free preparation from Nutritional Biochemicals Corporation, Cleveland, Ohio.

CARBOXYPEPTIDASE. Proteinase-free preparation as obtained from Nutritional Biochemicals Corporation, Cleveland, Ohio.

RESIN. Dowex 50W-X2 (200 to 400 mesh) obtained from J. T. Baker Chemical Co., Phillipsburg, New Jersey.

BUFFERS AND CHEMICALS for use with the Beckman/Spinco Amino Acid Analyzer as specified in the instruction manual (Spackman, 1960).

METHODS

OXIDATION. Tropomyosin was oxidized using the method of Hirs (1956) except that upon the completion of the action of performic acid, the solution was diluted with an equal volume of ice-water, and dialyzed overnight in the cold against flowing cold distilled water. This step removed the formic acid and

allowed the pH to rise to 3.0. The pH of the solution was further adjusted to 4.5 with 0.1*N* sodium hydroxide to precipitate the protein. The precipitated tropomyosin, separated by centrifuging, was washed thoroughly with cold distilled water. The oxidized tropomyosin so obtained was not dried; the wet precipitate was dissolved in the medium required by the following procedures.

CARBOBENZOXYLATION. The reaction of carbobenzoxy chloride with oxidized tropomyosin was carried out according to the method of Anfinsen *et al.* (1956). The rate of blocking of the free amino groups was measured by the ninhydrin test of Moore and Stein (1954). The resulting carbobenzoxy-tropomyosin (CBZ-tropomyosin) was completely precipitated with hydrochloric acid, centrifuged, separated by decantation and washed thoroughly with cold water.

TRYPTIC HYDROLYSIS OF CBZ-TROPOMYOSIN. CBZ-tropomyosin was made up to a 0.5% suspension in water. Tenth normal sodium hydroxide was added slowly over a period of 2 to 3 hours until the pH of the mixture reached and remained at 7.8. Crystalline trypsin in water (final concentration of 0.01%) was added to the preparation. Digestion was carried out at room temperature, with stirring and maintenance of the pH at 7.8 by the addition of 0.1*N* sodium hydroxide. The course of the digestion was followed by the removal of 0.1-ml samples at regular intervals for the ninhydrin test (Moore and Stein, 1954). After 8 hours the enzyme action was stopped by the addition of 0.2*N* hydrochloric acid to lower the pH to 3.5. There was little apparent solution of the CBZ-protein during the digestion. The preparation was centrifuged and separated by decantation to give an insoluble fraction and a soluble fraction. The insoluble material was washed thoroughly with water, absolute alcohol, and finally anhydrous ether. The soluble material was dried by evaporation under vacuum at room temperature.

DECARBOBENZOXYLATION OF CBZ-PEPTIDES. The carbobenzoxy-groups were removed from the ϵ-amino groups of the lysine residues with 30% hydrogen bromide in glacial acetic acid as described by Ben-Ishai and Berger (1952). The CBZ-free peptides were washed thoroughly with anhydrous ether and dried under vacuum over soda lime.

CHYMOTRYPTIC DIGESTION OF TROPOMYOSIN. Oxidized tropomyosin (1% by weight) was suspended in water, 0.005*N* in Ca^{++}, and the preparation was adjusted to pH 8.0 with 0.1*N* sodium hydroxide. In 1 to 2 hours, with stirring and further additions of alkali to maintain the pH at 8.0, the protein dissolved to give a clear solution. Chymotrypsin in water was added (final concentration of 0.02%), and the digestion allowed to proceed at room temperature, with stirring, and maintaining the pH at 8.0 by the automatic addition of 0.1*N* sodium hydroxide with a Radiometer titrator, model TTTla. The uptake of alkali was a measure of protein digestion; rapid for the first hour, then increasingly slower, until at the end of 6 hours, the digestion seemed complete (Fig. 1). At this time, 0.1*N* hydrochloric acid was added to lower the pH of the solution to 3.5. A small amount of precipitate which formed was removed by centrifugation. The solution of peptides was freeze-dried.

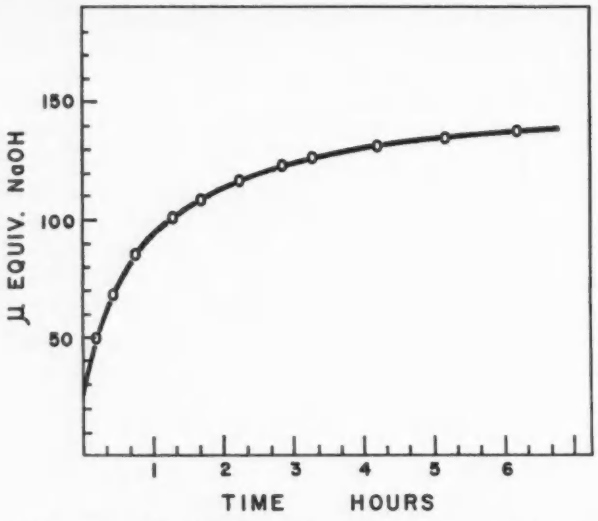

FIG. 1. The rate of hydrolysis of oxidized cod tropomyosin (1% solution) by α-chymotrypsin (0.02%) at pH 8.0 and 25°.

COLUMN CHROMATOGRAPHY OF PEPTIDES. The peptides were fractionated by ion-exchange chromatography. A column of Dowex 50W-X2 resin, 200 to 400 mesh, sodium form, 150 × 0.9 cm, water-jacketed for temperature control at 50°C, was connected to the Beckman/Spinco Amino Acid Analyzer. The resin was prepared according to the procedure of Moore and Stein (1954a), as modified by Hirs *et al.* (1956). Fifteen milligrams of the peptide mixtures, dissolved in 2 ml citrate buffer, pH 2.2, (sample diluent buffer), were added to the top of the column. Citrate buffers, pH 3.25, 4.25 and 5.28, normally used for amino acid analyses (Spackman *et al.*, 1958), eluted the peptides. Fractionation of the soluble peptides obtained by tryptic hydrolysis of CBZ-tropomyosin was carried out using the citrate buffers in sequence (Fig. 2). The peptides obtained by chymotryptic hydrolysis were separated by gradient elution. Two 500-ml flasks were connected in series to the column; the first contained citrate buffer, pH 3.25, and the second flask, citrate buffer at pH 5.28. As the 3.25 buffer was pumped into the column from the first flask, the displaced liquid was replaced by the 5.28 buffer from the second flask with mixing of the buffers by use of a magnetic stirrer (Fig. 3). In both cases, elution was continued until the 5.28 buffer did not separate more peptides as shown by the graph drawn by the Amino Acid Analyzer.

C-TERMINAL AMINO ACIDS. Carboxypeptidase digestion as described by Locker (1954).

N-TERMINAL AMINO ACIDS. The fluorodinitrobenzene procedure of Sanger (1945) as described by Fraenkel-Conrat *et al.* (1955). Identification of the DNP-amino acids was made by paper chromatography using 65:35 Skellysolve

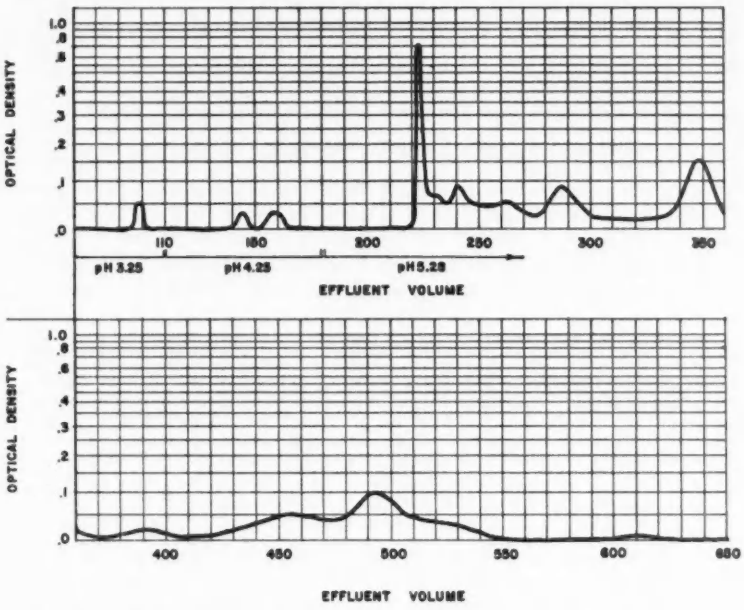

FIG. 2. Chromatogram of 15 mg soluble peptides, obtained from 8-hour tryptic digestion of carbobenzoxy-substituted oxidized cod tropomyosin, as recorded by the Beckman/Spinco Amino Acid Analyzer. The peptides were eluted from the column (150 × 0.9 cm) of Dowex 50W-X2 with citrate buffers: first, 110 ml at pH 3.25 containing 0.2*N* Na^+; then 70 ml at pH 4.25 containing 0.2*N* Na^+; and finally 470 ml at pH 5.28 containing 0.35*N* Na^+.

D–n-propanol saturated with 0.1*N* phthalate buffer pH 6.0, followed by 2.5*M* phosphate buffer, pH 6.0.

AMINO TERMINAL SEQUENCE. Edman (1950) degradation as described by Harris and Roos (1959) and modified for insoluble protein by Light and Smith (1960a).

RESULTS AND DISCUSSION

OXIDATION. A sample of the oxidized tropomyosin after acid hydrolysis was quantitatively analyzed for amino acids (Spackman *et al.*, 1958). This analysis showed that cystine had been converted to cysteic acid, methionine to the sulphone, and that the other amino acids, notably tyrosine, were present in the same ratios as in the original protein. A further sample of the tropomyosin was checked for the presence of N-terminal amino acids. As in the case of the native protein the result was negative, indicating that the oxidation had not broken the protein chain nor had it freed the N-terminal amino acid(s).

CARBOBENZOXYLATION, TRYPTIC DIGESTION AND DECARBOBENZOXYLATION OF THE SOLUBLE DIGEST. The addition of carbobenzoxy groups to the free,

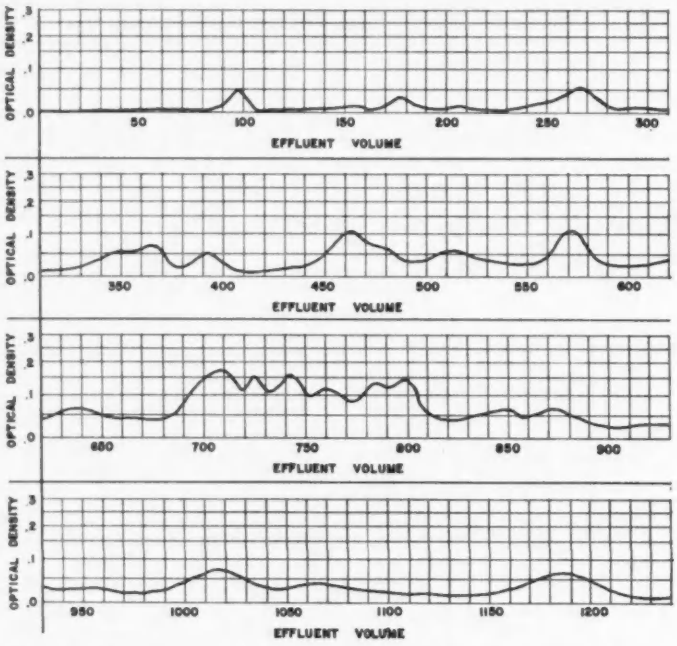

FIG. 3. Chromatogram of 15 mg soluble peptides, obtained from 6-hour α-chymotryptic digestion of oxidized cod tropomyosin, as recorded by the Beckman/Spinco Amino Acid Analyzer. Separation of the peptides on the column (150 × 0.9 cm) of Dowex 50W-X2 was effected by gradient elution with citrate buffers as described in the text.

ε-amino groups of lysine was followed by the ninhydrin reaction. Initially, the addition was rapid, and appeared complete at the end of 6 hours. Even after 24 hours, however, there was some colour yield with ninhydrin reagent. The CBZ-tropomyosin would not react with fluorodinitrobenzene, indicating that any ninhydrin-reacting amino groups were also blocked to that reagent. The CBZ-tropomyosin was relatively insoluble even in the sodium bicarbonate and precipitated completely in acid solution.

Due to the insoluble nature of the CBZ-tropomyosin even at pH 8.0, the trypsin digestion had to be carried out on a suspension of the material. The release of amino groups was slow as shown by the ninhydrin test, reaching its maximum after 7 to 8 hours. By weight, after the digestion, 15 to 20% of the material was now a soluble fraction, the remaining 80 to 85% was insoluble at pH 8.0; the exact amounts varied with the individual digestion. N-terminal amino acids were determined on both fractions to confirm the breakdown of CBZ-tropomyosin. The insoluble CBZ-peptides showed alanine, leucine, and lysine as N-terminal; the soluble fraction gave alanine, leucine, lysine, and valine. The two fractions were also analyzed for C-terminal amino acids in order to

check the specificity of the trypsin digestion. As expected, arginine was found to be C-terminal in both cases. The insoluble fraction also showed a strong isoleucine reaction, suggesting the presence of the carboxyl end of the protein chain and/or unchanged tropomyosin. Isoleucine is the C-terminal acid of cod tropomyosin (Hoogland *et al.*, 1961). After these trypsin digestion studies had been discontinued in favour of an initial digestion with α-chymotrypsin, De Milstein and Bailey (1961) reported that trypsin would not completely digest unsubstituted invertebrate tropomyosin; a "tryptic core" remained which accounted for approximately one-half of the molecule. After treatment of the insoluble peptides with hydrobromic acid to remove the CBZ-groups (Ben-Ishai and Berger, 1952), the product remained insoluble in aqueous solution between pH 2.0 and 9.0. No further work was done on this fraction. The soluble peptides, after removal of the CBZ-groups, were separated by ion-exchange chromatography.

CHYMOTRYPTIC DIGESTION. The course of the digestion of oxidized tropomyosin with α-chymotrypsin is shown in Fig. 1. After hydrolysis, 95% by weight of the original material was soluble between pH 2.0 and 8.0. The insoluble portion of the digest was discarded; the soluble portion was fractionated by chromatography.

COLUMN CHROMATOGRAPHY OF THE DIGESTS. The separation of soluble peptides obtained by tryptic digestion of CBZ-tropomyosin is shown in Fig. 2. At least 12 peptides were separated; one, extremely acidic in nature, 3 neutral and at least 8 basic. In spite of the inadequate action of the trypsin and the variation in the exact amount of the soluble portion of the digest, the composition of this soluble portion of four digests was found to be reproducible.

To effect the separation of the peptides of the chymotryptic digest, gradient elution was used since the sudden change of buffer from pH 3.25 to pH 4.25 appeared to elute a number of peptides with the buffer front. By this method at least 34 peptides could be detected in the chymotryptic digest (see Fig. 3). The chymotryptic hydrolysis of tropomyosin and the separation of the peptides contained in three separate digests were also reproducible.

In Fig. 2 and 3, it should be noted that the area of the peptide peaks is determined by the number of free amino groups and the curves represent the reaction of ninhydrin with unhydrolyzed peptides. For further sequence studies, the connection of a large preparative column and a stream divider to the Analyzer would allow the separation and detection of the peptides in one operation. This would eliminate testing a portion of each fraction with ninhydrin although it would probably be necessary to check the fractions, after alkaline hydrolysis, of an initial run with ninhydrin (Hirs *et al.*, 1956), to ensure that all the peptides present can in fact be detected automatically.

The specificity of the action of trypsin on carbobenzoxy-substituted tropomyosin can be questioned. With the lysine residues of the protein blocked with the CBZ-groups, trypsin should break only bonds involving arginine, so that cod tropomyosin with 22 arginine residues (Hoogland *et al.*, 1961) should yield 23 peptides. The eluate from one column separation was collected in

fractions and the peptides were checked for size by ninhydrin after alkaline hydrolysis. Excepting the strongly acidic peptide and the first basic peptide, all appeared to be small, made up of 2 to 5 amino acid residues. If the trypsin digestion had broken bonds involving only arginine, then 11 of the 22 arginine residues of tropomyosin would have to be relatively close together in the molecule. Unfortunately the insoluble nature of 80% of the trypsin digest prevents the easy study of this fraction in order to determine if the remaining 11 arginine residues are widely spaced over the remainder of the protein chain.

α-Chymotrypsin is known to hydrolyze peptide bonds containing an aromatic amino acid, i.e., phenylalanine, tyrosine, and tryptophan, as well as some leucine and methionine bonds. Theoretically, cod tropomyosin with 2 phenylalanine, 8 tyrosine, no tryptophan, 10 methionine and 53 leucine residues (Hoogland *et al.*, 1961) could yield a minimum of 11 and a maximum of 74 peptides. Assuming that the average pK of the liberated amino groups is near 8.0 and that the molecular weight of the tropomyosin is 52,500 (Hoogland *et al.*, 1961), by calculation from the total alkali used (Fig. 1), approximately 37 peptide bonds were hydrolyzed. Certainly some of the 34 peptides separated after chymotrypsin digestion could contain more than one peptide but it would appear that approximately one-third of the leucine and methionine bonds were hydrolyzed under these conditions.

In summary, α-chymotrypsin which solubilizes 95% of oxidized tropomyosin would appear to be a logical choice of enzyme for the initial digestion of this protein for amino acid sequence studies. The specific action of trypsin for bonds involving arginine and lysine residues could be used to better advantage in the study of peptides obtained by an initial hydrolysis of the protein with α-chymotrypsin.

N-TERMINAL AMINO ACID ANALYSIS. After this work had been terminated, Saad and Kuminz (1961) reported that rabbit tropomyosin, native and oxidized, when dissolved in 6*M* urea and treated with 1-fluoro-2,4-dinitrobenzene at 50° gave glutamic acid as the N-terminal amino acid in molar quantities (M.W. = 60,000). The dinitrophenyl derivatives of serine and alanine were also obtained in quantity; DNP-serine and DNP-alanine were obtained in 4 to 5 times greater yield (0.4 and 0.5 moles respectively) from the oxidized than from the native protein. This result could not be duplicated with cod tropomyosin. Paper chromatographic analysis of the acid hydrolysate of dinitrophenylated cod tropomyosin (Fraenkel-Conrat *et al.*, 1955) prepared in 6*M* urea at 50° gave only trace quantities of glutamic acid, alanine, lysine, and leucine. The same result was obtained using either oxidized or native protein. Light and Smith (1960a), using the phenylisothiocyanate procedure for N-terminal amino acid analysis, reported the N-terminal sequence of papain after solution of the protein in 6*M* urea. Cod tropomyosin dissolved in 6*M* urea and treated with phenylisothiocyanate in the same manner gave no phenylthiohydantoin derivatives as shown by the UV spectrum of the extract.

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The Relict Fauna of Greiner Lake, Victoria Island, N.W.T., Canada[1]

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ABSTRACT

A survey of Greiner Lake in Victoria Island revealed the presence there of four species usually considered to be 'relicts' of marine or glacial events. The species are: *Mysis relicta*, *Limnocalanus macrurus*, *Gammaracanthus loricatus aestuariorum* and *Mesidothea* (*Saduria*) *entomon*. *M. entomon* is a new record for fresh waters isolated from contact with the sea in North America and *G. loricatus aestuariorum* is a new record for this region. Greiner Lake (15 m above sea level) is in an area that has risen from the sea within the last 1,300 years. It has a maximum depth of 11 m and a maximum summer temperature of approximately 8°C. An analysis of the lake water is given and also a brief account of other species present. Possible methods for the arrival of the relicts in Victoria Island are discussed.

INTRODUCTION

It has been recognised that certain species occurring discontinuously in fresh waters of Northern Europe and Asia and the Caspian Sea have relatives in arctic marine or brackish conditions. The affinity of these freshwater species to those occurring in the sea and the manner in which they assumed their present locations has given rise to considerable discussion and speculation. Of the 8 species usually considered, 6 are crustaceans, one is a seal, *Phoca hispida*, and one a fish, *Myoxocephalus quadricornis*. Segerstråle (1957) had divided these species into two groups:

Group I — *Mysis relicta*, *Pontoporeia affinis*, *Limnocalanus macrurus* (and the completely freshwater species *Pallasea quadrispinosa* on account of similarities in distribution).

Group II — *Gammaracanthus lacustris*, *Mesidothea* (*Saduria*) *entomon*, *Myoxocephalus quadricornis* and *Phoca hispida*.

The distribution of the animals in Group II is restricted to areas that have been subjected to marine inundation at some former time, whereas those of the first group have a wider distribution, but are confined to waters that have been connected with proglacial lakes (Högbom, 1917; Ricker, 1959). For a more extensive treatment reference should also be made to Holmquist (1959), Segerstråle (1957), Lomakina (1952) and Ekman (1920).

The use of the word 'relict' has been questioned by Holmquist, especially for *Mysis relicta*, on the ground that there is no evidence for a former, more widespread, distribution of which the present populations are a remnant. Her objections appear to have considerable validity but no alternative term was

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suggested. It seems useful to retain the term 'relict' without too rigid a definition, unsatisfactory though this may be, until the position of these species is clarified.

In North America only four of the so-called relict species have previously been described from fresh water without direct access to the sea, although the complete list of related marine species is present along the arctic coast. The species described from fresh water are: *Mysis relicta*, *Pontoporeia affinis*, *Limnocalanus macrurus* and *Myoxocephalus thompsoni*. Ricker has established that all the fresh waters in which *M. relicta* and *P. affinis* occur are the remnants of proglacial lakes, with the exception of Nuwuk Pond, Alaska; however this body of water has recently been shown (Mohr *et al.*, 1961) to have a hypersaline bottom layer. *Myoxocephalus thompsoni* has a similar distribution, although not so extensive, to that of the previous two species: its status and origin have been discussed by McAllister (1959). *Limnocalanus macrurus* is widespread in the fresh waters of North America and Greenland (Wilson, 1959).

During the course of a fishery survey conducted by J. G. Hunter and the author at Cambridge Bay, Victoria Island, in the summer of 1961, Greiner Lake was surveyed and found to contain 4 relict species: *Gammaracanthus loricatus*, *Mysis relicta*, *Mesidothea entomon* and *Limnocalanus macrurus*.

Since the history and distribution of these species is closely bound up with events since the Pleistocene it is necessary to consider the geology of the area in which they are found.

GEOLOGY OF VICTORIA ISLAND

Victoria Island is the largest land mass in the western Canadian Archipelago, covering an area of 220,000 square kilometres (85,000 square miles) (Fig. 1). The extensive lowlands in the south and east are made up of Paleozoic limestone rocks covered with glacial drift. There is a gradual rise of land from the southeast to the northwest; north of a line running from Hadley Bay to Prince Albert Sound there is a well defined Precambrian upland region (Dunbar and Greenway, 1956). The highest elevations in the lowland area probably reach 455 m (1,500 ft) although the detailed topographical survey is not yet complete (Dept. of Mines and Technical Surveys, 1956).

The drainage of the lowlands shows the extremely complex character of a recently glaciated landscape. In general there is a radial pattern of streams, many of which do not flow continuously thoughout the summer, interconnecting innumerable lakes, many of considerable size (Ferguson, 740 km^2; Washburn. 292 km^2). In the centre of this region are the remains of a former glacial lake; several unnamed lakes occur in this locality and form the headwaters of rivers flowing to both the north and south coasts.

Much of the land in the southeast corner and most of the coastline has been inundated in post glacial times (Wilson *et al.*, 1958). Washburn (1947) surveyed the area in some detail and showed that Mount Pelly (203 m), near Cambridge Bay, has strand-lines in a remarkably good state of preservation up to a height of 153 m. This amount of submergence indicates a former ice-cover to a depth

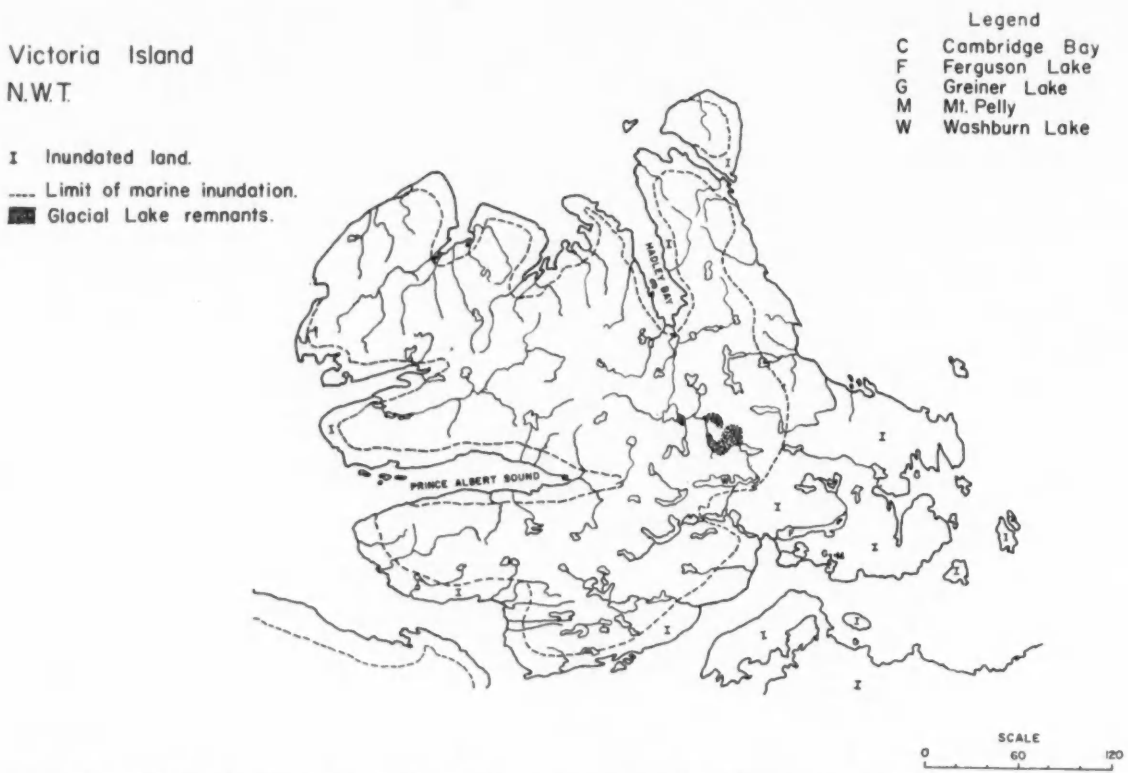

FIG. 1. Victoria Island showing the distribution of inland waters and the limit of marine inundation. After Dunbar and Greenaway (1956) and Wilson *et al.*, (1958).

of 550 m, although differences in sea-level may require a revision of this figure. Associated with the strand-lines are the remains of the marine pelecypods *Astarte borealis*, *Saxicava arctica*, *Mya truncata*, *Macoma calcarea* and *Cardium ciliatum*, the barnacle *Balanus* sp. and the gastropod *Acmea testudinalis*. This association is quite comparable with the present day *Macoma* communities described by Ellis (1960) for low-arctic conditions (temperature above 0°C) in waters 5 to 20 m deep. Owing to the state of preservation of the strand-lines Washburn concludes that the ice conditions during the period of emergence were different from those at present, due either to much less ice movement or a warmer climate with consequent absence of ice. There is also evidence that the rise of land relative to the ocean took place without warping since the level of the strand-lines varies as little as ± 3.2 cm per km (5 in per mile).

The spacing between the strand-lines indicates a fairly uniform rate of elevation, and, by their state of preservation, a relatively rapid rise. As a result of a survey of Cambridge Bay Harbour made in 1853 by Collinson, Washburn has been able to arrive at an estimate of the actual rate at which the land was elevated. Collinson charted a shoal 2 ft (61 cm) below the surface in an unambiguous location; this shoal is now a small island with a minimum emergence at highest high-tide of 33 cm. No information on the state of the tide is given by Collinson so that an accurate computation is not possible, however it appears that the land has risen a possible maximum of 1,810 cm and a minimum of 1,100 cm up to 1947, the date of Washburn's observations. This gives a maximum rate of rise of 1.96 m and a minimum of 1.16 m per 100 years. Indirect evidence for the rate of elevation is given by Gibson (1939) who shows that former villages of the Thule Eskimo culture, now well above sea-level, were originally sited at the water's edge. Gibson concludes "we may reasonably speculate that the land has risen approximately 50 ft in the last 1,000 years". This is in very good agreement with the median figure derived from Collinson's observations.

LIMNOLOGY

Greiner Lake (Fig. 2), situated at an elevation of 15 m above sea level under the western end of Mount Pelly, is the final lake in a system that surrounds the mountain. Discharge from the lake is via the 4 km of Freshwater Creek into the head of Cambridge Bay. The highest lake levels occur immediately after break-up, following which there is a gradual fall of about 60 cm through the open water season. Break-up occurs about the third week in June and in 1961 ice cover had been achieved by the second week in September, giving approximately 80 days of open water. Surface temperatures were taken from the second week in August until freeze-up. The maximum temperature of 8°C was attained in early August and maintained until the last week of this month, when there was a rapid fall to zero. During the winter it is reported that ice forms to a thickness of 2 m.

The lake covers an area of 46.8 km^2; it is generally shallow with an average depth of 5 m and a maximum depth of 11 m (Fig. 2). Most of the shore line

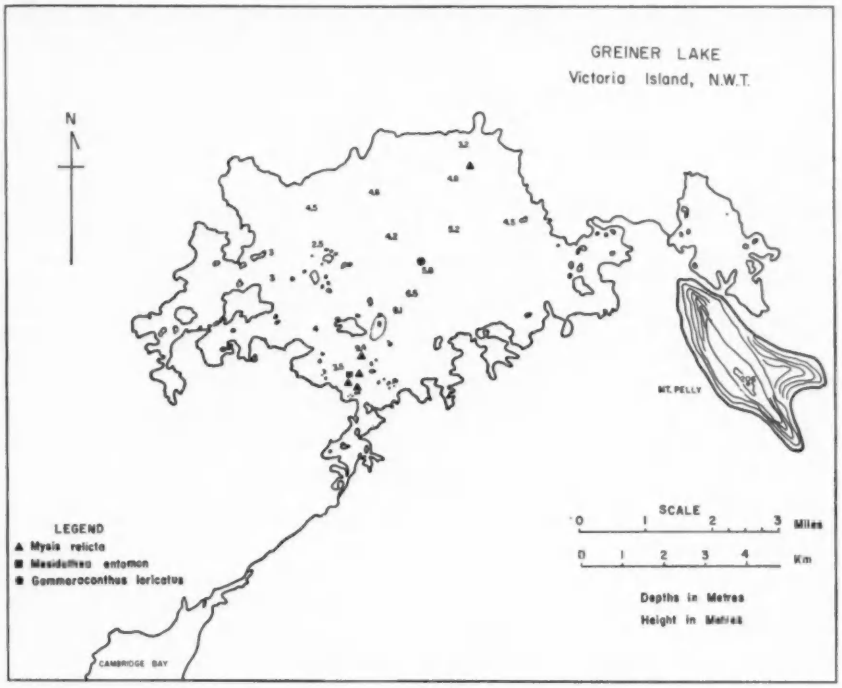

FIG. 2. Greiner Lake, showing the depths and localities in which the relicts were captured.

is rocky to a depth of 4 to 5 m, below which there is a fairly flat bottom of mud and silt; on the south side the shore shelves rapidly due to the effect of ice during break-up, whereas on the north side the slope is very gradual.

Throughout the summer of 1961 strong winds blew almost constantly, eliminating any possibility of stratification or oxygen deficit at any depth.

A complete water analysis is given in Table I, which was obtained when possible sources of drinking water were being investigated for the settlement at Cambridge Bay. The analysis was carried out by Mr R. Holowaty of the Department of National Health and Welfare, Public Health Engineering Division, Edmonton, Alberta.

The inorganic salt content of the lake is fairly high when compared with oligotrophic lakes but it is well within the normal range of alkaline fresh waters (Hutchison, 1957).

The relatively high content of dissolved salts allows for considerable productivity in the short summer season, which causes some colouring of the water. Visibility in August is approximately 2 m through the water. Much of the lake bottom is covered with the alga *Cladophora* which in parts forms mats 5 cm thick. Other macroscopic plants present in some quantity are the globose colonies of the blue-green alga *Nitella* and the aquatic moss *Camptothecium*.

TABLE I. Water analysis of Greiner Lake, from a sample taken 11th April, 1959. Analysis carried out by R. Holowaty, Department of National Health and Welfare. ppm = parts per million by weight.

pH	7.4	Sulphate	5.3 ppm
Total hardness (Ca plus Mg)	119.4 ppm	Chloride	21.0 ppm
Alkalinities		Nitrate	0.58 ppm
Phenolphthalein as $CaCO_3$	Nil	Fluoride	2.0 ppm
Methyl orange as $CaCO_3$	114.0 ppm	Alumina and iron oxide (R_2O_3)	0.2 ppm
Iron (total)	Nil	Loss on ignition (1 hr at 500°C)	10.0 ppm
Colour (Hazen)	Less than 0.5	Total dissolved solids	
Turbidity	1.0	Calculated	155.1 ppm
Calcium	23.1 ppm	Determined	156.4 ppm
Magnesium	15.0 ppm	Nitrate nitrogen	0.13 ppm
Sodium (Calculated)	12.0 ppm	Nitrite nitrogen	0.001 ppm
Bicarbonate as CO_3	68.4 ppm	Free ammonia nitrogen	0.013 ppm
Carbonate	Nil	Albuminoid nitrogen	0.092 ppm

FISH FAUNA

Two species of fish dominate the vertebrate population: arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*). Part of the char population migrates to the sea at the time of break-up in June, returning to the lake in the third week of August. During their feeding migration to the sea they are taken in some numbers by the local native and sport fishermen. The lake trout also support a small native fishery during the winter months.

In addition to these, ninespine sticklebacks (*Pungitius pungitius*) and lake herring (*Leucichthys sardinella*) were taken, the latter in very small numbers.

INVERTEBRATES

The invertebrate fauna was sampled through the use of a 6-in Ekman dredge, plankton hauls (No. 20 net), a 1-m stramin net towed behind a small boat with a powerful outboard motor, and the extensive sampling of lake trout stomachs.

The following species of crustaceans have so far been identified:

Anostraca	*Branchinecta paludosa*
Notostraca	*Lepidurus arcticus*
Amphipoda	*Gammaracanthus loricatus aestuariorum*
Isopoda	*Mesidothea entomon glacialis*
Copepoda	*Limnocalanus macrurus*
Mysidaceae	*Mysis relicta*

In addition, bottom sampling yielded several species of chironomid and caddis larvae, and the plankton hauls a very numerous species of calanoid copepod, a cyclopoid copepod and a species of *Daphnia*.

Of 191 lake trout stomachs examined 69 (36.1%) were empty, 64 (33.5%) contained *Lepidurus arcticus*, apparently the dominant source of fish food during

August, 24 (12.6%) contained *Mysis relicta* and 7 (3.7%) contained amphipods subsequently identified as *Gammaracanthus loricatus*, similarly 1 stomach contained the remains of an isopod *Mesidothea entomon*. Eighteen dredge samples were taken, of which 4 included *M. relicta*, 1 contained *M. entomon* and 1 had 4 very young amphipods 2–3 mm in length. Four *M. relicta* were the only specimens taken in the stramin net hauled at a depth of 1–2 m below the surface at a speed

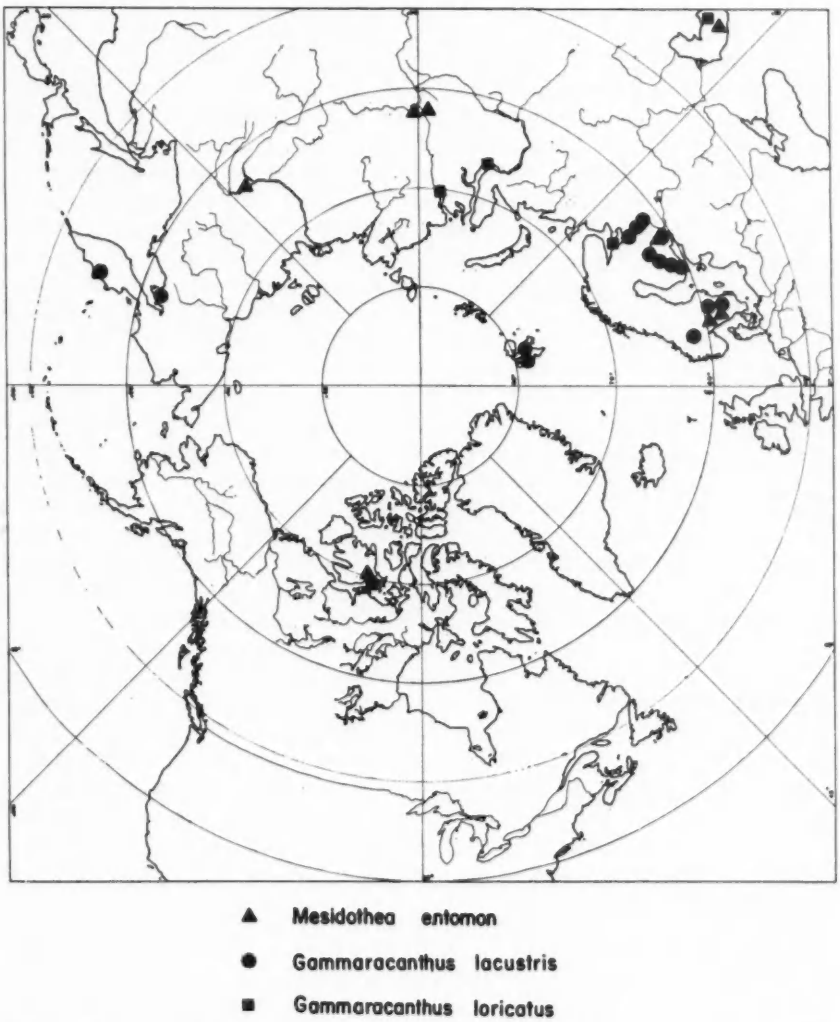

FIG. 3. Distribution of *Gammaracanthus loricatus aestuariorum*, *G. lacustris* and *Mesidothea entomon* in inland waters.

of approximately 10–12 km per hour. *Limnocalanus macrurus* was taken in all plankton hauls.

In addition to these specimens from Greiner Lake, the neighbouring, and much larger, Ferguson Lake yielded collections of *M. relicta* and *G. loricatus* from lake trout stomachs. Six of the fish examined had been feeding heavily on *M. relicta* and the remnants of G. *loricatus* were recovered from 2 more.

CONSIDERATION OF THE RELICT SPECIES

Gammaracanthus loricatus (Sabine) subsp. *aestuariorum* Lomakina 1952

The marine distribution of *G. loricatus* is arctic circumpolar with several records in Canadian arctic waters (Dunbar, 1954; Shoemaker, 1920); it has also been taken within 3 degrees of the north pole as part of the under-ice epifauna (Barnard, 1959). Lomakina (1952) defined the upper limit of salinity tolerance of this species in Russian waters as being between 25 and 30 parts per thousand. The Canadian arctic collections made by the M.V. *Salvelinus* of the Fisheries Research Board of Canada have indicated that the normal habitat of the species lies in salinities between 20.43 and 32.45 parts per thousand (unpublished data).

In inland waters the distribution is exceedingly sporadic (Fig. 3), records having been obtained from southern Norway and Sweden (Sars, 1893), the Karelian Isthmus (Segerstråle, 1957; Lomakina, 1952), Spitzbergen (Olofson, 1918), the Caspian Sea (Sars, 1927), Central Siberia (Lomakina, 1952) and Kamchatka (Derjavin, 1923). The authors quoted do not necessarily represent the first or only workers on *Gammaracanthus* in the area concerned.

Sars (1895) originally recognised the relationship between the marine and freshwater forms of *Gammaracanthus*; he divided the genus into two species, *G. loricatus* (marine) and *G. relictus* (freshwater). This division has not been generally accepted even with the correction of the name of the freshwater species to *G. lacustris*; neither Stevenson (1940), Ekman (1940) nor Thienemann (1950) give the lacustrine form full specific status, referring to it as *G. loricatus* var. *lacustris*.

Lomakina (1952) in the most recent study of the genus retains the two species but subdivides *G. loricatus*: *G. loricatus loricatus* (marine), *G. l. ostiorum* (White Sea estuaries), *G. l. aestuariorum* (Siberian estuaries) and *G. l. caspius* (Caspian Sea). However from the published description it is not possible to differentiate between *G. l. ostiorum* and *G. l. aestuariorum*; the situation is further complicated by conflict between the description of *G. l. aestuariorum* given by Lomakina (1952) and that of Gurianova (1951) — who largely follows an earlier work of Lomakina (unpublished dissertation of 1950) — particularly in the shape of the rostrum which is used as one of the main diagnostic characters.

Lomakina (1952) considers that certain changes have taken place, particularly in the relative size and shape of the gnathopods and the posteroventral angle of the third epimeral plate, during the transition from the marine environment to fresh water. The sequence is shown in Fig. 4 with drawings of the corresponding parts of the Greiner Lake material (Fig. 5). In *G. l. loricatus* gnathopod I is longer than gnathopod II and in *G. lacustris* the situation is reversed. The

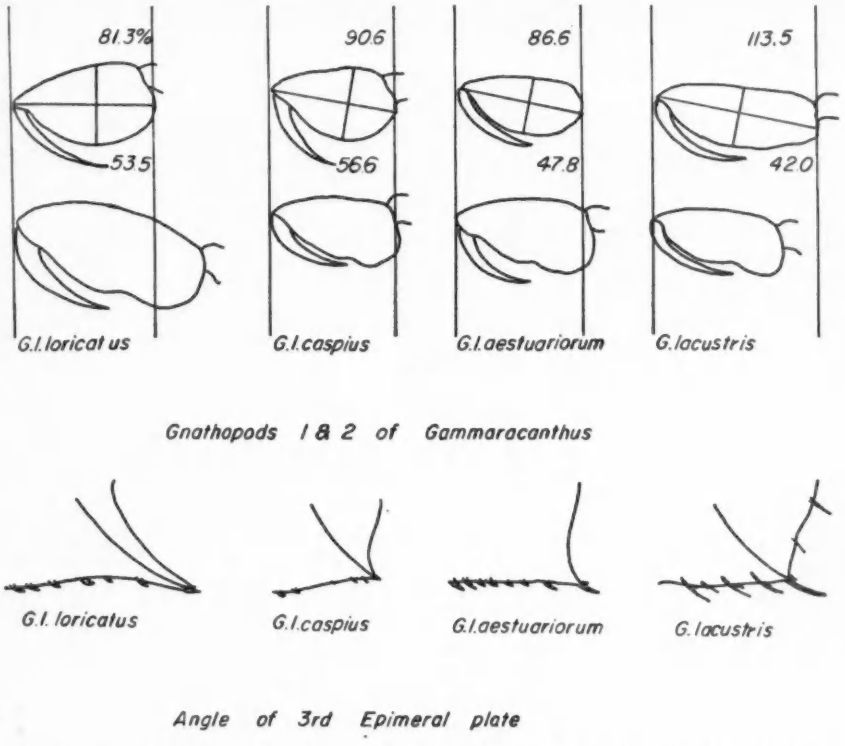

FIG. 4. Gnathopods I and II and posteroventral angle of epimeral plate III of *G. l. loricatus*, *G. l. caspius*, *G. l. aestuariorum* and *G. lacustris*. From Lomakina, 1952.

posteroventral angle of epimeral plate III in *G. l. loricatus* is acute (41°) and in *G. lacustris* it is almost square with an angle of 107°. The estuarine forms are intermediate in these characters, the gnathopods being nearly equal in length and the epimeral plate angle being 70°.

The rostrum of *G. l. aestuariorum* is, according to Lomakina (1952), "... shorter than in *G. l. loricatus* usually it is equal to or less than the first segment of antenna I and it is noticeably curved". Gurianova (1951) describes the rostrum of *G. l. aestuariorum* as "... straight or slightly curved".

The Greiner Lake specimens (Fig. 6) appear to agree closely with the description given by Lomakina, apart from some differences in the shape of the gnathopods in which they more closely resemble those of the Caspian Sea type. The main affinities seem to lie with the specimens from the Siberian estuaries and so the Greiner Lake specimens are tentatively assigned to the subspecies *Gammaracanthus loricatus aestuariorum*. However the material available is so restricted that rigorous morphological conclusions cannot yet be drawn.

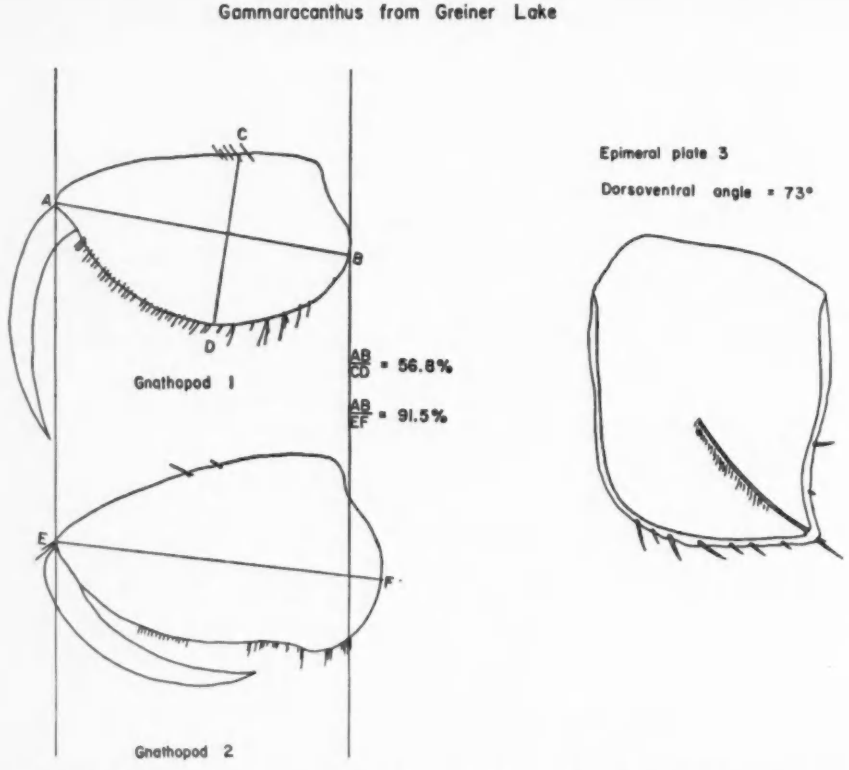

FIG. 5. Gnathopods and epimeral plate III of *Gammaracanthus loricatus aestuariorum* from Greiner Lake.

The collection of young amphipods in Greiner Lake, whilst not positively identifiable as *Gammaracanthus*, is certainly indicative of breeding taking place there since no other amphipods were collected.

It is of great interest that one specimen of *G. loricatus aestuariorum* identical with those from Greiner Lake was collected in the Beaufort Sea off Warren Point on the Tuktoyaktuk Peninsula, at a depth of 2 m in a salinity of 6.3‰ at a temperature of 9°C (F.R.B. of Canada, unpublished data). This subspecies has not previously been recorded from the sea in North America.

Mysis relicta Lovén 1861

The world distribution of this species in fresh water is much wider than that of *Gammaracanthus* (see Holmquist, 1959, p. 188). It was originally assumed by Lovén (1862) that *M. relicta* had originated from the marine *M. oculata* through having been left behind when the sea retreated from the land around the Baltic, acquiring tolerance to fresh water at the same time. This theory has

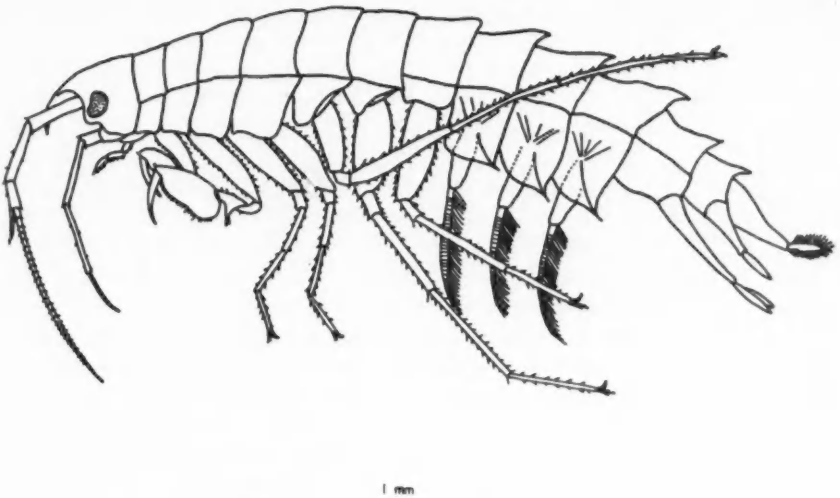

FIG. 6. *Gammaracanthus loricatus aestuariorum* from Greiner Lake. (Drawing by the author.)

subsequently been modified especially for those species in Segerstråle's Group I. For these species Högbom's "sluicing-up" process in front of the advancing or retreating ice-cap is more generally accepted. Holmquist however, considers that *M. relicta* is a good freshwater species of pre-Pleistocene origin, whose occurrence in the sea is infrequent but whose spread has been greatly facilitated by ". . . floods, submersions and .transgressions". Holmquist has also shown that the morphology of *M. relicta* is not affected by changes in salinity. However it would seem probable that *M. relicta* can disperse through a saline medium in that it is occasionally found in marine conditions. The nearest marine record to Victoria Island is off the Alaskan coast at Point Barrow (Mohr, 1953).

The species of *Mysis* from Greiner Lake is undoubtedly *relicta*, specimens having been checked by Dr Holmquist. It is apparently fairly abundant, occurring in 20% of the lake trout with food in their stomachs. In Ferguson Lake it appears to be an appreciable item in the diet to judge by the numbers contained in some stomachs. In Greiner Lake it was taken in 20% of the bottom samples in water between 5.2 and 8.4 m deep, and also in stramin net hauls at a depth of 1 to 2 m. It is thus apparent that at this time of the year it is both benthic and pelagic.

Mesidothea entomon (L.) subsp. *glacialis* Gurianova 1933

The distribution of this species is in many ways comparable with that of *Gammaracanthus*. It is partly circumpolar in the sea, but with a discontinuity in the Greenland-Iceland area. In fresh water it is only found in isolated localities (Fig. 3). There is apparently general agreement that the same species is found in both marine and freshwater habitats. The subspecies *M. entomon*

entomon is found in the fresh waters of the Karelian Isthmus and also in the White Sea; the subspecies *M. entomon glacialis* is similarly found in the rivers of Siberia and also along the coast at their outflows (Gurianova, 1933). *M. entomon glacialis* and *M. sibirici* occur along the North American coast, the former predominating westwards from the Mackenzie Delta at least as far as Baillie Island.

The single specimen collected in Greiner Lake was taken in an Ekman dredge sample in 5.2 m. It is an immature individual with a length of 12 mm. From various body measurements it is apparently very close to the subspecies *M. e. glacialis* (J. R. Bray, personal communication).

Limnocalanus macrurus Sars 1863

This copepod is of relatively common occurrence in the lakes of North America, from the northeastern United States west to Wisconsin, through Canada, Alaska and Greenland, to northern Europe and the Caspian Sea. The marine ancestor has been postulated to be *L. grimaldii* by Ekman (1907) and this view is shared by Segerstråle, although the latter author considers this species to have a brackish water habitat rather than one truly marine.

L. grimaldii was collected off Collinson Point, Alaska, by the Canadian Arctic Expedition (Willey, 1920) but has not been taken subsequent to this date in North American waters.

Specimens of the Greiner Lake material have been checked by Dr Holmquist. In this locality it is relatively abundant, being taken in all plankton hauls; specimens averaged 2 mm in length. No maturing females were observed.

DISCUSSION

Because of the limited data on the distribution of these new records, it is not intended to comment in detail on their bearing on general theories of relict distribution. However it is considered useful to discuss the salient features, in order to stress the important contribution which studies of Victoria Island relicts could make.

Considerable controversy has been aroused over the time and the locality of the origin of relict species. Holmquist considers *M. relicta* to be of pre-Pleistocene origin with no significant marine history in recent times. Ricker produces evidence for marine centres of dispersal for North American *M. relicta* and *P. affinis*. Segerstråle favours a single occurrence of the acquisition of freshwater tolerance with subsequent spread through a freshwater medium. McAllister (1959) advances the suggestion that *Myoxocephalus quadricornis* migrated "voluntarily" into fresh water from the Gulf of St. Lawrence and Hudson Bay, probably in pre-Pleistocene times, its later spread being facilitated by glacial events.

The main factors to be established in order to provide a firm base for theories of relict origin and distribution are: 1) the relationship of the marine species to their freshwater counterparts; 2) if a marine origin can be established, then did

a single or multiple invasion of fresh water occur. These factors should be considered for individual species, and it should not be assumed that all the relicts have a similar history. There is also the suggestion of Hutchinson (1960) to be considered that "... the final physiological adaptation, to water containing less than say 10 mg Cl per litre or about 0.002 percent sodium chloride salinity, can only occur with the development of a really efficient salt uptake mechanism. Coastal fresh waters, enriched with NaCl from sea spray, would support less efficient salt absorbers than would inland fresh waters. But the investigator who relied on his tongue as an analytical instrument would class both sets of waters as fresh." It would be of great interest to know the full extent of the ability of relict species to take up chlorine ions in dilute solution.

Victoria Island was apparently completely glaciated during the Pleistocene (Wilson *et al.*, 1958); following reduction of the ice the land has risen a minimum of 153 m. This implies a complete repopulation of the island since the end of the glacial period. There is no suggestion of a possible land bridge that would have facilitated the process of repopulation; in fact it must be concluded that the straits separating the island from the mainland have gradually narrowed with the emergence of land on both sides (Wilson *et al.*, 1958; Bird and Bird, 1961).

The relicts occur in a region that has been elevated from the sea within the last 850 to 1,300 years so it seems possible that each species may have arrived in one of three ways. The most obvious is that they were left behind when, as a result of emergence, the marine-brackish conditions gave way to fresh water. This method would seem the most probable for *Gammaracanthus loricatus aestuariorum* and *Mesidothea entomon glacialis*, in that both these species have been found in the sea at Warren Point; no records exist which would indicate a possible centre of dispersal on the mainland. A second alternative is that some of the relicts may have entered from the mainland using the sea as a medium for dispersal; this would include Holmquist's suggestion that *M. relicta* can be transported on icefloes in the manner of "erratics", and their passage through the upper, less saline layers of the Arctic Ocean. Finally there is the possibility that they entered by way of a proglacial lake stretching to the mainland, the remnants of which still exist in the centre of the lowland region of the island (Fig. 1). As far as is known there is no evidence to suggest that this lake was of such extent, but in view of the close relationship between the distribution of *M. relicta* and the existence of proglacial lakes the possibility cannot be ignored. Such a theory is more attractive when applied to *M. relicta* and *L. macrurus* than when applied to the other two species.

The first two alternative methods, depending on the sea for dispersal, would limit the present distribution to a level below the limit of the marine transgression unless upstream migration has taken place. In view of the limited swimming powers of *M. relicta* (cf. Holmquist, p. 185), probably the most active of the species concerned, this is not likely to be extensive. If, on the other hand, animals reached Victoria via a proglacial lake, colonization would be from the centre and new habitats could be invaded as land arose from the sea and waters freshened. Such a condition would be indicated by a uniform distribution of the

species over the whole of the lowland area, and particularly significant would be their occurrence in the central glacial lake remnant.

Apart from the relict species discussed above, the presence of lake trout, and to a less extent the lake herring, requires explanation. Authentic records of lake trout in the Archipelago exist only from Southampton and Victoria Islands and possibly Banks Island. It is reasonable to suppose that trout could navigate the Dolphin and Union Strait in spring when surface waters are at their least saline; however, if this is so, why is their spread so restricted, and why, for instance, has Baffin Island not been invaded? Lake herring tend to be anadromous in the arctic so that no great difficulty is presented in crossing from the mainland; but again, this species is not recorded from the other islands.

Species that are conspicuous by their apparent absence in Victoria are *Myoxocephalus quadricornis* and *Pontoporeia affinis*. Both occur in the North American arctic sea; *M. quadricornis* is abundant in the brackish waters at the head of Cambridge Bay, and *P. affinis* has been recorded by Shoemaker (1920) for Alaska and by Dunbar (1954) for Ungava Bay. *P. affinis* also occurs in Great Bear Lake, which is the nearest known continental record for *M. relicta*.

This discovery of 'relict' species on Victoria Island provides an excellent opportunity to study the invasion under well defined historical conditions. When a more complete picture of the distribution of both relicts and lake trout has been obtained in this and other islands of the Archipelago, it should be possible to make comparisons between the various species which will throw considerable light on the original path of invasion.

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Machine Computations of Mass Transport in the North Pacific Ocean[1]

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ABSTRACT

Recently, a series of computer programs was developed by the Fisheries Research Board of Canada Pacific Oceanographic Group to enable more intensive studies to be carried out of the effects of winds over the ocean surface on the circulation in the ocean. The programs are used to compute geostrophic velocities and mass transports from oceanographic station data, Ekman and total transports from mean sea-level atmospheric pressure.

The theoretical background for the programs is developed and examples of the results obtained are given. More complete discussions of the results will be given as processed information is accumulated.

A MAJOR OBSTACLE to the utilization of oceanographic and meteorological data for the study of currents in the oceans has been the enormous amount of manual computation required to process the initial data. With the advent of high-speed digital computers, this obstacle has been practically overcome so that comprehensive and systematic studies of currents and transports can now be made with comparative ease.

The Fisheries Research Board of Canada Pacific Oceanographic Group has been processing routine oceanographic data on a digital computer (ALWAC III-E) for the past 3 years. Recently, programs were constructed to compute geostrophic velocity and transport from oceanographic station data, and transport from estimated mean surface winds over the ocean (Fofonoff and Froese, MS, 1960; Froese, MS, 1960). These programs allow more detailed studies to be made of the relation between atmospheric and oceanic circulation.

The theoretical background for the computer programs is given in the present paper, together with descriptions of the programs and examples of the results obtained. Discussion of the significance of the computed results is deferred until sufficient processed data become available.

SIMPLIFIED THEORY OF STEADY-STATE TRANSPORTS

Studies carried out by Shtokman (1946), Sverdrup (1947), Stommel (1948) and Munk (1950) have lead to the development of a simple theoretical model of steady wind-driven ocean circulation. The model is constructed by assuming a balance in the horizontal plane of Coriolis force and forces due to pressure and stress gradients. Horizontal acceleration terms are neglected and vertical forces

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are assumed to be in hydrostatic equilibrium. The model is applicable to interior regions of the ocean. More complete equations are necessary for the western boundary region to include the phenomena of westward intensification (Stommel, 1948).

The simplified equations expressing the balance of forces in the horizontal plane are:

$$-\rho f v = -\frac{\partial p}{\partial x} + \frac{\partial \tau_x}{\partial z} \tag{1}$$

$$\rho f u = -\frac{\partial p}{\partial y} + \frac{\partial \tau_y}{\partial z} \tag{2}$$

where ρ is density, f the coriolis parameter, p the pressure, and u and v, τ_x and τ_y, are the components of velocity and stress in the x–y plane. The co-ordinates are chosen to form a right-handed system with the positive x–axis directed eastward, the y–axis northward, and the z–axis upward, with the origin at the mean free surface of the ocean.

Equations (1) and (2) can be written in vector form by introducing a velocity vector $\mathbf{v}$, a stress vector $\boldsymbol{\tau}$ and a unit vector $\mathbf{k}$ directed parallel to the positive z–axis. In vector notation (1) and (2) become:

$$\rho f (\mathbf{k} \times \mathbf{v}) = -\nabla p + \frac{\partial \boldsymbol{\tau}}{\partial z} . \tag{3}$$

In addition, the motion satisfies the equation of mass continuity:

$$\nabla \cdot \rho \mathbf{v} = \frac{\partial \rho u}{\partial x} + \frac{\partial \rho v}{\partial y} + \frac{\partial \rho w}{\partial z} = 0, \tag{4}$$

where w is the vertical component of velocity. The pressure is given by the hydrostatic equation:

$$\frac{\partial p}{\partial z} = -\rho g, \tag{5}$$

where g is gravitational acceleration.

The equations for the transport components are obtained by integration of the equations with respect to depth.

Let $\mathbf{V}$, with components U, V, represent the mass transport through a section of unit horizontal width, defined by:

$$\mathbf{V} = \int_{z_B}^{z_S} \rho \mathbf{v} \, dz \tag{6}$$

where z_S and z_B are the surface and bottom of the ocean respectively, and are both functions of x and y. Integrating (4) with respect to depth yields:

$$\int_{z_B}^{z_S} \nabla \cdot \rho \mathbf{v} dz = \nabla \cdot \mathbf{V} + \rho_S (w_S - \mathbf{v}_S \cdot \nabla z_S) - \rho_B (w_B - \mathbf{v}_B \cdot \nabla z_B) = 0. \tag{7}$$

Assuming that losses of water through the surface and bottom are negligible, (7) can be reduced to:

$$\nabla \cdot \mathbf{V} = 0. \tag{8}$$

Integrating (3) yields:

$$f(\mathbf{k}\times\mathbf{V}) = -\nabla\int_{z_B}^{z_S} p\,dz + p_S\nabla z_S - p_B\nabla z_B + \tau_S - \tau_B. \tag{9}$$

The integral of pressure in (9) can be expressed in two different, but equivalent, forms that aid in the interpretation of the term. If E_p is introduced for the potential energy of a column of water relative to the bottom of the ocean, i.e.:

$$E_p = \int_{z_B}^{z_S} (\Phi - \Phi_B)\,\rho\,dz, \tag{10}$$

where Φ is the gravitational potential (geopotential), the integral of pressure can be written:

$$\int_{z_B}^{z_S} p\,dz = E_p + p_S\,(z_S - z_B) \tag{11}$$

provided vertical variations of gravity are neglected. The pressure at the surface, p_S, may be set equal to zero with negligible error. The integral then reduces to the potential energy as defined in (10).

An alternative interpretation of the pressure integral is obtained by the transformation:

$$\int_{z_B}^{z_S} p\,dz = \frac{1}{g}\int_0^{p_B} p\alpha\,dp = \frac{1}{g}\int_0^{p_B} p\alpha_0\,dp + \frac{1}{g}\int_0^{p_B} p\delta\,dp \tag{12}$$

where α_0 is the specific volume at a constant reference temperature and salinity, and a function of pressure p, and δ is the anomaly of specific volume $\alpha - \alpha_0$. Introducing the geopotential anomaly ΔD, defined by:

$$\Delta D = \int_0^p \delta\,dp, \tag{13}$$

the integral in (12) can be converted to:

$$\int_{z_B}^{z_S} p\,dz = \frac{1}{g}\int_0^{p_B} p\alpha_0\,dp + \frac{1}{g}\int_0^{p_B}\left[\Delta D_B - \Delta D\right]dp = E_p^0 + \chi \tag{14}$$

where

$$E_p^0 = \frac{1}{g}\int_0^{p_B} p\alpha_0\,dp \tag{15}$$

is a function of p_B only, and

$$\chi = \frac{1}{g}\int_0^{p_B} p\delta\,dp = \frac{1}{g}\int_0^{p_B}\left[\Delta D_B - \Delta D\right]dp \tag{16}$$

is defined as the *anomaly of potential energy.*

In terms of (15) and (16), (9) becomes:

$$f(\mathbf{k}\times\mathbf{V}) = -\nabla E_p^0 - \nabla\chi - p_B\nabla z_B + \tau_S - \tau_B. \tag{17}$$

Using the fact that E_p^0 is a function of p_B only, the gradient of E_p^0 can be replaced by:

$$\nabla E_p^0 = \frac{\partial E_p^0}{\partial p}\nabla p_B = \frac{p_B\alpha_0}{g}\left[\nabla_z p_B - \rho_B g\nabla z_B\right]. \tag{18}$$

Assuming that $\rho_B\alpha_0 \doteq 1$, (17) may be written

$$f(\mathbf{k}\times \mathbf{V}) = -p_B\alpha_0\nabla_z p_B - \nabla\chi + \tau_S - \tau_B \tag{19}$$

where ∇_z implies differentiation holding $z_B(x, y)$ constant, i.e., $\nabla_z p_B$ is the horizontal gradient of pressure at the bottom.

If the bottom stress is assumed to be negligible, the velocity at the bottom will be given by the geostrophic equation:

$$\rho_B f\,(\mathbf{k}\times \mathbf{v}_B) = -\nabla_z p_B. \tag{20}$$

The transport produced by a constant velocity equal to the bottom velocity is:

$$\int_{z_B}^{z_S} \rho \mathbf{v}_B\, dz = \frac{p_B \mathbf{v}_B}{g} = \mathbf{V}_B, \tag{21}$$

so that

$$f(\mathbf{k}\times \mathbf{V}_B) = -\frac{p_B\alpha_B}{g}\nabla_z p_B \doteq -\frac{p_B\alpha_0}{g}\nabla_z p_B, \tag{22}$$

assuming $\alpha_0 \doteq \alpha_B$.

The transport $\mathbf{V}_B$ will be called the *barotropic transport*. The transport relative to the deep-water flow, satisfying the equation:

$$f(\mathbf{k}\times \mathbf{V}_g) = -\nabla\chi \tag{23}$$

will be termed the *baroclinic transport*. Similarly, the transport satisfying the equation:

$$f(\mathbf{k}\times \mathbf{V}_E) = \tau_S \tag{24}$$

is termed the *Ekman transport*. Using these definitions of transport components, (19) may be reduced to:

$$\mathbf{V} = \mathbf{V}_B + \mathbf{V}_g + \mathbf{V}_E \tag{25}$$

provided bottom stress is neglected. Thus, in the steady state, the total transport can be divided into three parts related to the deep water circulation, the density field, and surface stresses due to wind. The three parts of the total transport are shown schematically in Fig. 1.

Of the three transport components given in (25), only $\mathbf{V}_g$ is obtainable from standard observations of physiçal structure in the ocean. The Ekman transport must be evaluated from estimates of surface wind stress. The barotropic transport depends on deep-water circulation and is extremely difficult to determine. Only recently have techniques been developed (Swallow, 1955) to make reliable velocity measurements in deep water. The task of determining the deep-water circulation over a large expanse of ocean is still a formidable one.

The baroclinic transport $\mathbf{V}_g$ is determined by both the Ekman transport and the deep-water circulation. The curl of (22), (23) and (24) yields:

$$f\nabla\cdot\mathbf{V}_E + \beta V_E = \mathrm{curl}_z\tau_S \tag{26}$$

$$f\nabla\cdot\mathbf{V}_g + \beta V_g = 0 \tag{27}$$

$$f\nabla\cdot\mathbf{V}_B + \beta V_B \doteq -\rho_B f\,(\mathbf{v}_B\cdot\nabla z_B) \tag{28}$$

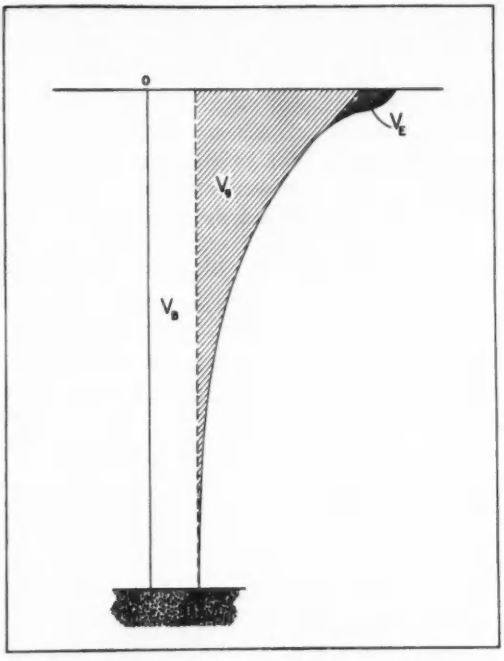

FIG. 1. Schematic diagram showing the separation of total transport into barotropic (V_B), baroclinic (V_g) and Ekman (V_E) transport components. Transports are proportional to the areas enclosed by the velocity profile as indicated.

where $\beta = df/dy$ is the rate of variation of the Coriolis parameter with latitude. Addition of (26), (27) and (28) and substitution of (8) yields:

$$\beta V = \text{curl}_z \tau_S - \rho_B f (\mathbf{v}_B \cdot \nabla z_B). \tag{29}$$

The influence of wind stress and bottom topography on the transport components is shown in equations (26) and (28). As the total divergence of the transport is zero from (8), the divergence of the baroclinic transport is determined once the wind stress and deep-water circulation are known. Hence, both the baroclinic and total transports can be determined from (27) and (29).

The deep circulation cannot be specified within the limits of the present elementary model. This can be seen by splitting the baroclinic transport into two parts, such that each satisfies an equation similar to (27). The transport components may then be divided into two systems; one giving the wind-induced circulation, the other representing an arbitrary internal mode of flow. Clearly, an internal mode transports heat and salt and is, therefore, strongly dependent on thermodynamical processes in the ocean. However, as no sources or sinks of energy for the internal mode are included in the present model, the theory of

this mode is not developed further. It is pointed out, however, that the baroclinic transports calculated from oceanographic station data may include transport due to an internal mode. The baroclinic transport, in this case, cannot be entirely accounted for in terms of surface wind stress. As a starting point for a study of the correlation between atmospheric and oceanic circulation, it is necessary to assume that the internal mode of circulation can be neglected in comparison with the wind-induced mode. This is equivalent to assuming that the velocities in the deep water are so small that they may be neglected.

COMPUTER PROGRAMS FOR MASS TRANSPORT

The transport components described in the previous Section can be estimated from either meteorological or oceanographic data. A set of computer programs have been developed to enable either computation to be carried out on an ALWAC III-E digital computer.

The programs consist of four sections:

(*a*) processing of standard oceanographic station data,
(*b*) computation of potential energy anomaly,
(*c*) computation of geostrophic velocity and mass transport, and
(*d*) computation of geostrophic and total transport from estimated surface wind stress.

Programs for (*a*), (*b*) and (*c*) are designated to operate with identical input tapes containing oceanographic data at observed depths. Programs for (*d*) are independent of the programs for the other items and use sea-level atmospheric pressure as input data.

(*a*) Standard Oceanographic Station Data

The computer program now being used to process standard station data has been described by Froese (MS, 1960). Basically, the program consists of the interpolation of temperature, salinity, and dissolved oxygen concentration at standard depths and the computation of additional quantities such as sound velocity, sigma-*t* (σ_t), dynamic height, potential temperature, and potential energy anomaly. These computations are made routinely on all station data and the results are offset-reproduced for rapid distribution[2].

The input tapes contain information of the following sequence for each station:

Station number, time (GMT), date (day, month, year), latitude, longitude, sounding (fm), weather, wind (direction, speed), air temperature (dry, wet), barometer (mb), cloud (type, amount) sea (direction, coded height), swell (direction, coded height), visibility of Secchi disc (m), followed by depth, temperature, salinity and dissolved oxygen concentration at each depth.

A copy from a typical input tape giving the input format is shown in Fig. 2. The input is terminated by the code letter (e) following the last digit of the station data. Provision is made to label second and third casts if desired. Missing data are coded by inserting dashes (–) in place of the missing values.

[2]Manuscript Report Series (Oceanographic and Limnological), 1957 *et seq.*, Fisheries Research Board of Canada, Pacific Oceanographic Group, Nanaimo, B.C.

```
 2
1821   3-vii-60   48 50n  128 40w  1200
01  320  6  55 50  1032  8n 3c   6  320 2   260 1   10

0000  1310 31937 ---
0010  1305 32238 557
0020  1210 ----- ---
0030  1170 32604 581
0050  0946 32692 592
0075  0833 32779 579
0100  0805 33056 485
0125  0790 33386 386
0150  0778 33664 296
0175  0751 33812 245
0200  0704 33909 217
0250  0636 33971 181
0300  0583 34011 145
0395  0512 34069 095
0498  0449 34175 043
0748  0390 34313 021
0998  0329 34420 028
1000  ---- ----- ---e
```

FIG. 2. Input format for oceanographic station data. Station number is given first followed by time, date, latitude longitude, depth to bottom, weather, wind direction and speed, barometric pressure, cloud types and total amount, direction and height of sea and swell and Secchi-disc reading. Depth, temperature and oxygen are given at each observed depth. Missing observations are coded by dashes (–) and input is terminated by a code letter (e). Units and headings for the station are contained in the computer program (see Fig. 3).

All of the headings, except for page number and some symbols not present on the typewriter keyboard, are contained in the program and are inserted in their appropriate location during output in the format required for the data record as shown in Fig. 3. In addition to the observed data, the computer

```
                                STATION    2

TIME: 1821  DATE:  3-vii-60  LAT: 48° 50' N, LONG: 128° 40' W, BOTTOMED: 1200 fms.
WEATHER: 01  WIND: Dir. 320°  Speed  6  AIR TEMP: Dry 55°  Wet 50°  BARO: 1032.  mb.
CLOUD: Type 8n 3c Amt.  5  SEA: 320°-2   SWELL: 260°-1   SECCHI DISC: 10 m.

Depth      Temp.        S                    S/V       D.O.
 m.          °C         ‰          t        ft/sec    mg.at/l

0000       13.10     31.937      24.03      4912.3     .535*
0010       13.05     32.238      24.27      4913.4     .557
0020       12.10     32.452*     24.62      4904.1     .571*
0030       11.70     32.604      24.81      4900.7     .581
0050       09.46     32.692      25.26      4875.6     .592
0075       08.33     32.779      25.50      4865.4     .579
0100       08.05     33.056      25.76      4862.5     .485
0125       07.90     33.386      26.04      4865.3     .386
0150       07.78     33.664      26.28      4864.3     .296
0175       07.51     33.812      26.43      4865.0     .245
0200       07.04     33.909      26.58      4858.8     .217
0250       06.36     33.971      26.72      4853.2     .181
0300       05.83     34.011      26.81      4849.3     .145
0395       05.12     34.069      26.95      4845.7     .095
0498       04.49     34.175      27.10      4843.6     .043
0748       03.90     34.313      27.27      4850.9     .021
0998       03.29     34.420      27.42      4857.6     .028
1000       03.29*    34.421*     27.42      4857.7     .028*


                          INTERPOLATED DATA

Depth      Temp.        S                    S/V       D.O.        D         P.E.      Pot.Temp.
 m.          °C         ‰          t        ft/sec    mg.at/l                              °C

0000       13.10     31.937      24.03      4912.3     .535      00.000    000.00      13.10
0010       13.05     32.238      24.27      4913.4     .557      00.038    000.02      13.05
0020       12.10     32.452      24.62      4904.1     .571      00.073    000.07      12.10
0030       11.70     32.604      24.81      4900.7     .581      00.106    000.16      11.70
0050       09.46     32.692      25.26      4875.6     .592      00.165    000.39      09.46
0075       08.33     32.779      25.50      4865.4     .579      00.231    000.81      08.32
0100       08.05     33.056      25.76      4862.5     .485      00.291    001.35      08.04
0125       07.90     33.386      26.04      4865.3     .386      00.345    001.96      07.89
0150       07.78     33.664      26.28      4864.3     .296      00.392    002.63      07.77
0175       07.51     33.812      26.43      4865.0     .245      00.435    003.34      07.49
0200       07.04     33.909      26.58      4858.8     .217      00.474    004.10      07.02
0250       06.36     33.971      26.72      4853.2     .181      00.547    005.77      06.34
0300       05.83     34.011      26.81      4849.3     .145      00.614    007.65      05.80
0400       05.09     34.075      26.95      4845.5     .092      00.737    012.04      05.05
0500       04.48     34.176      27.10      4843.7     .043      00.846    017.08      04.45
0600       04.22     34.238      27.18      4846.2     .033      00.946    022.69      04.17
0700       04.00     34.290      27.24      4849.3     .025      01.039    028.92      03.94
0800       03.76     34.338      27.31      4852.1     .023      01.127    035.70      03.70
1000       03.29     34.421      27.42      4857.7     .028      01.288    050.47      03.21
```

FIG. 3. Output format for oceanographic station data for input shown in Fig. 2. The symbols σ and Δ are not contained on the Flexowriter keyboard and are entered manually in the headings for sigma-t (column 4) and dynamic height (column 7).

calculates values of σ_t and sound velocity at observed depths and performs interpolations on missing data. The interpolated values at observed depths are tagged by an asterisk to identify them in the output. Values of temperature, salinity, and dissolved oxygen are interpolated for standard depths. These interpolated values are used to compute σ_t, sound velocity, dynamic height, potential energy anomaly and potential temperature.

A logarithmic interpolation is used to obtain values at standard depths. For example, if z_1 and z_2 are observed depths with temperatures T_1 and T_2 respectively, the interpolated temperature T at depth z, such that $z_2 > z > z_1$, is

$$T = (T_2 - T_1) \log \left[\frac{z + 10}{z_1 + 10}\right] \Big/ \log \left[\frac{z_2 + 10}{z_1 + 10}\right] + T_1. \qquad (30)$$

The depth z is increased by 10 m to allow extrapolation to the surface when necessary.

The logarithmic interpolation has several advantages over the three-point Lagrangian interpolation (Fofonoff and Tabata, MS, 1958). Only two observed depths are required, so that the depth interval between observations is not as critical as it is in the three-point interpolation. Moreover, the logarithmic interpolation does not introduce spurious maxima or minima in the vicinity of thermoclines and haloclines. Its accuracy is comparable to the three-point interpolation in the deeper water where the change in seawater characteristics in the North Pacific Ocean is roughly proportional to the logarithm of depth (Tully, 1957).

A simplification has been introduced in the computation of sound velocity and dynamic height by introducing a formula for pressure in terms of depth. A study (Fofonoff and Froese, MS, 1960) of the pressure change with depth as computed by integration of the hydrostatic equation has shown that the seasonal and regional variation of pressure at the standard depths is not larger than 0.5 decibar. Hence the pressure can be computed to sufficient accuracy by a simple polynomial in terms of depth. The use of the pressure formula reduces the amount of computation about 30% for each station by eliminating integration of the hydrostatic equation. The empirical pressure formula used for the North Pacific is:

$$p_{(\text{decibar})} = 1.00721\, z + 2.57 \times 10^{-6} z^2$$

where z is in metres, with gravity = 981.00 cm/sec^2.

The dynamic height is calculated from the formula:

$$\Delta D = \int_0^p \delta \mathrm{d}p \simeq \Sigma \frac{1}{2} (\delta_i + \delta_{i-1}) (p_i - p_{i-1}). \qquad (31)$$

An advantage in calculating the dynamic height ΔD in terms of the pressure interval $(p_i - p_{i-1})$ rather than the depth interval $(z_i - z_{i-1})$ is that the formula does not involve gravity explicitly. Variations of gravity can then be taken into account in the pressure formula. Similarly, the formula for velocity of sound is expressed in terms of pressure rather than depth so that cumbersome latitude factors are avoided.

To facilitate analysis of mass transport, a computation of potential energy anomaly:

$$\chi = \frac{1}{g}\int_0^p p\delta dp \doteq \frac{1}{2g}\sum (p_i\delta_i + p_{i-1}\delta_{i-1})\,(p_i - p_{i-1}) \tag{32}$$

has been added to the program. Geostrophic mass transport ψ_g is related to differences in χ by the equation:

$$\psi_g = \frac{\chi_2 - \chi_1}{f} \tag{33}$$

where χ_2 and χ_1 are values of the potential energy anomaly at a given standard depth for a pair of stations, and f is the Coriolis parameter at the mean latitude of the two stations.

(*b*) Potential Energy Anomaly

The program for computing potential energy anomaly is essentially an abbreviated form of the standard station program. It is designed for high-speed computation of the anomaly only. All other computations are deleted from the program. The purpose of this program is to allow a large number of stations to be processed for the study of the distribution and variation of baroclinic transport in the ocean.

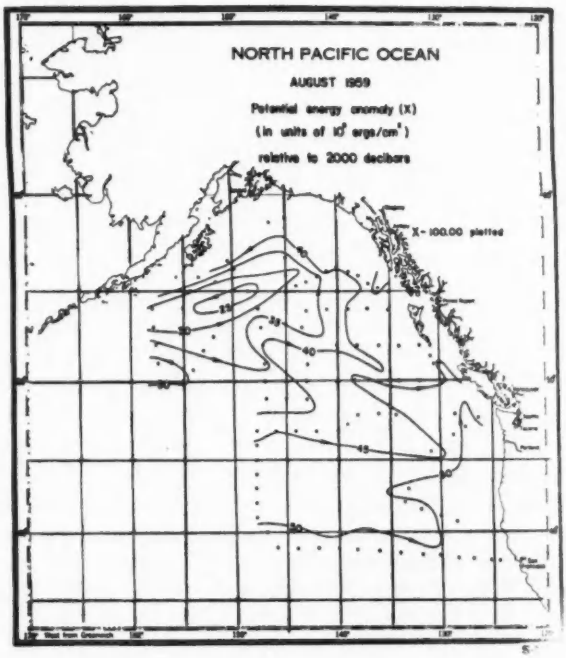

Fig. 4. Distribution of potential energy anomaly for the northeastern part of the North Pacific Ocean. Transport between contours is about 4 to 5 million metric tons per second, depending on latitude.

A typical distribution of potential energy anomaly relative to the 2000-decibar surface in the northeastern Pacific Ocean, is shown in Fig. 4. The baroclinic transport in the Gulf of Alaska is about 15 to 20 million metric tons/sec.

(*c*) GEOSTROPHIC VELOCITY AND MASS TRANSPORT

A program has been constructed to compute the mean geostrophic velocity and mass transport between pairs of oceanographic stations, from the temperature and salinity at observed depths.

Observations of temperature and salinity at a series of depths suffice to evaluate ΔD at a particular location in the ocean. If ΔD is known at two points, the mean geostrophic velocity v_{gn}, normal to the line joining the two points, is:

$$v_{gn}(0) - v_{gn}(p) = \frac{\Delta D_1(p) - \Delta D_2(p)}{fL} \tag{34}$$

where L is the distance between the points, and f is the average value of the Coriolis parameter. A positive value indicates a velocity component to the right of the direction from point (1) to point (2).

If (ϕ_1, λ_1) and (ϕ_2, λ_2) are the latitudes and longitudes in degrees of the two points, the distance L between them is given approximately by:

$$L = \frac{\pi R}{180}\left\{(\phi_2 - \phi_1)^2 + \cos\phi_2 \cos\phi_1 (\lambda_2 - \lambda_1)^2\right\}^{\frac{1}{2}} \tag{35}$$

where R is the mean radius of the earth. The distance between points in a 10° grid is given to within 0.1% by (35).

The computer program accepts input data from a pair of stations and computes the geostrophic velocity difference $v_{gn}(0) - v_{gn}(p)$ given by (34) at each standard depth and the geostrophic mass transport ψ_S relative to each standard depth z_S, where:

$$\begin{aligned}\psi_S &= L\int_0^{z_S} \bar{\rho}\left[v_{gn}(p) - v_{gn}(p_S)\right]dz \\ &= L\int_0^{z_S} \bar{\rho}\left\{\left[\frac{\Delta D_1(p_S) - \Delta D_1(p)}{\bar{f}L}\right] - \left[\frac{\Delta D_2(p_S) - \Delta D_2(p)}{\bar{f}L}\right]\right\}dz \\ &= \frac{1}{\bar{f}}\left[\chi_1(p_S) - \chi_2(p_S)\right].\end{aligned} \tag{36}$$

The geostrophic velocity profile can be obtained by plotting $v_{gn}(0) - v_{gn}(p_S)$ against depth. A sample calculation using this program is given in Fig. 5. The geostrophic velocity profile, relative to the 1000-decibar surface, is shown in Fig. 6. The program was constructed by modifying the standard station program already described. After computations are completed, the data for the second of a pair of stations are transferred to memory locations occupied by the first station. Thus, a third, or a sequence of stations, can be processed to yield geostrophic velocity and transport between each consecutive pair of stations.

(*d*) GEOSTROPHIC AND TOTAL MASS TRANSPORT FROM SURFACE WIND STRESS

The simplified model of steady-state ocean circulation can be used to estimate transport components from the distribution of wind stress over the surface of

Station Positions:
006 LAT 47°41' LONG 129°09' W
007 LAT 47°49' LONG 131°05' W

Depth	Velocity	Transport
metres	cm/sec	10⁶ metric tons/sec
0010	000.0913	00.00067
0020	000.1742	00.00252
0030	000.2562	00.00556
0050	000.4162	00.01507
0075	000.5155	00.02426
0100	000.1480	-00.02369
0150	-000.5933	-00.16171
0200	-000.5519	-00.15084
0250	-000.4425	-00.11407
0300	-000.2688	-00.04278
0400	-000.0681	00.06204
0500	-000.0146	00.09797
0600	000.1066	00.19758
0700	000.2278	00.31524
0800	000.3766	00.48201
1000	000.6392	00.83521
1200	000.8534	01.15459
1500	001.0641	01.62033
2000	001.1831	01.93188
2500	001.0049	01.32991

FIG. 5. Geostrophic surface velocity and mass transport relative to pressure surfaces at each standard depth to 2500 m. The stations were occupied in March 1958. Geostrophic velocity profile with depth is obtained by subtracting the velocity at each depth from the velocity at the reference depth.

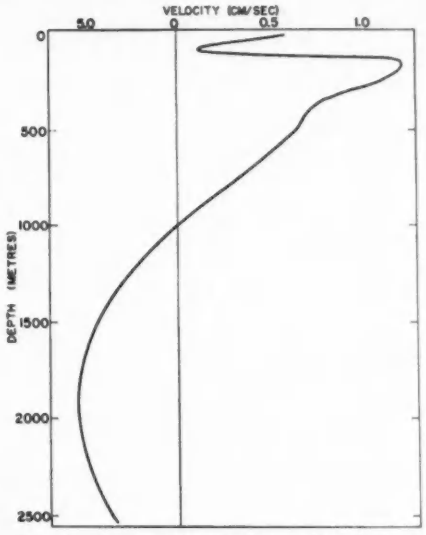

FIG. 6. Geostrophic velocity profile relative to the 1000-decibar surface obtained from calculations shown in Fig. 5.

the ocean. Direct measurements of surface stress or even surface winds are not available. An indirect method, similar to that used by Montgomery (1935), is used to obtain approximate estimates of the stress components in terms of geostrophic winds calculated from the mean atmospheric pressure distribution. Charts of monthly mean sea-level atmospheric pressure for the northern hemisphere, issued by the Extended Forecast Section of the United States Weather Bureau, provide the basic meteorological data required for the calculations. The monthly mean atmospheric pressures are obtained by averaging pressures read twice daily from synoptic charts at a regular set of grid points covering the northern hemisphere. The pressures are interpolated to a standard grid consisting of alternate points of a 5° grid in latitude and longitude. Pressures from the region 10°N to 65°N and 115°E to 105°W covering the North Pacific Ocean (Fig. 12) are used in the calculations of the transport components. The input format for atmospheric pressure is shown in Fig. 7 and the grid pattern used in the computations in Fig. 8. Computed values of pressure and transport components are typed from the output tapes directly onto special charts as illustrated in Fig. 9.

Computations are performed in a spherical co-ordinate system in terms of latitude (ϕ) and longitude (λ). First, the zonal and meridional components of geostrophic wind at sea level are calculated using the equations

$$u_g = -\frac{1}{\rho_a f R}\frac{\partial p_a}{\partial \phi} \tag{37}$$

$$v_g = \frac{1}{\rho_a f R \cos\phi}\frac{\partial p_a}{\partial \lambda} \tag{38}$$

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FIG. 7. Monthly mean sea-level atmospheric pressures over the North Pacific Ocean. Pressures are recorded in 0.1-millibar (mb) units as anomalies from 1000 mb if greater or equal to 1000 mb, and from 900 mb if less than 1000 mb. Zeros are inserted at grid points not entering into the computations. Output format for pressure is given in Fig. 12.

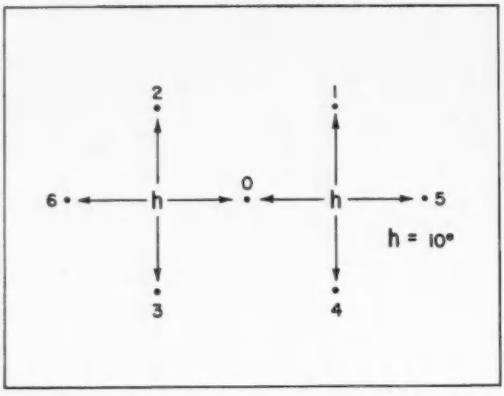

FIG. 8. Computational grid pattern used for estimating surface stress and transport components from the mean sea-level atmospheric pressure distribution.

where R is the earth's radius, p_a mean sea-level atmospheric pressure, ρ_a mean atmospheric density and f the Coriolis parameter. Surface winds are obtained by a rotation of the geostrophic wind vector by an angle θ (positive for deviations to the right of the downwind direction) and a change of magnitude by the ratio r. The transformation equations to obtain surface winds are:

$$u_S = r\,(\cos\theta\, u_g + \sin\theta\, v_g)$$
$$v_S = r\,(-\sin\theta\, u_g + \cos\theta\, v_g). \tag{39}$$

Surface stress τ_S is estimated by a square-law formula of the form:

$$\tau_S = \rho_a C_D |\mathbf{v}_S| \mathbf{v}_S \tag{40}$$

where ρ_a is mean atmospheric density, C_D a constant drag coefficient and $\mathbf{v}_S$ is the surface wind velocity vector.

The components of surface wind stress are:

$$\tau_\lambda = \rho_a C_D\,(u_S^2 + v_S^2)^{\frac{1}{2}}\, u_S$$
$$\tau_\phi = \rho_a C_D\,(u_S^2 + v_S^2)^{\frac{1}{2}}\, v_S. \tag{41}$$

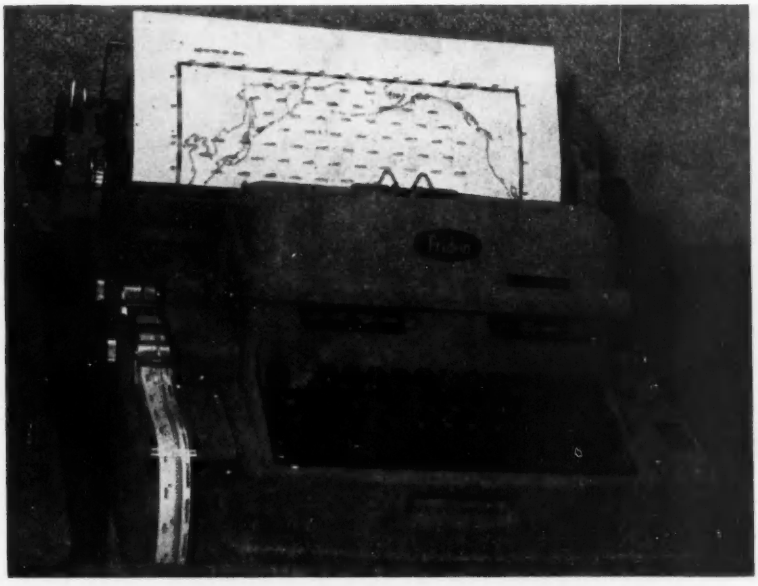

FIG. 9. Illustration of the method of preparing transport charts from computer tapes. Charts are specially prepared to align with the spacing and carriage action of the Flexowriter.

Both components are evaluated and used to compute the components of Ekman transport:

$$U_E = \tau_\phi / f$$
$$V_E = -\tau_\lambda / f. \tag{42}$$

The meridional component of total transport V is given by:

$$V = R \frac{\text{curl}_z \boldsymbol{\tau}_S}{\partial f / \partial \phi}$$
$$= -\frac{\rho_a C_D}{\cos^2\phi (u_S^2 + v_S^2)^{\frac{1}{2}}} \left\{ (2u_S^2 + v_S^2) \frac{\partial v_S}{\partial \phi} + u_S v_S \frac{\partial v_S}{\partial \phi} - u_S (u_S^2 + v_S^2) \sin\phi \right.$$
$$\left. - (u_S^2 + 2v_S^2) \frac{\partial v_S}{\partial \lambda} - u_S v_S \frac{\partial u_S}{\partial \lambda} \right\}. \tag{43}$$

The horizontal surface wind velocity gradients in (43) are evaluated in terms of the corresponding geostrophic wind gradients by differentiating the transformation in (39) with respect to latitude or longitude, e.g.:

$$\frac{\partial u_S}{\partial \phi} = r \cos\theta \frac{\partial u_g}{\partial \phi} + r \sin\theta \frac{\partial v_g}{\partial \phi}. \tag{44}$$

The gradients of geostrophic velocity in turn can be expressed in terms of first and second-order derivatives of pressure. Thus,

$$\frac{\partial u_g}{\partial \phi} = -\frac{1}{\rho_a f R}\left[\frac{\partial^2 p_a}{\partial \phi^2} - \cot\phi \frac{\partial p_a}{\partial \phi}\right]$$

$$\frac{\partial v_g}{\partial \phi} = \frac{1}{\rho_a f R}\left[\sec\phi \frac{\partial^2 p_a}{\partial \phi \partial \lambda} - \frac{1 - 2\sin^2\phi}{\sin\phi \cos^2\phi} \frac{\partial p_a}{\partial \lambda}\right]$$

$$\frac{\partial u_g}{\partial \lambda} = -\frac{1}{\rho_a f R} \frac{\partial^2 p_a}{\partial \phi \partial \lambda}$$

$$\frac{\partial v_g}{\partial \lambda} = \frac{1}{\rho_a f R}\left[\frac{1}{\cos\phi} \frac{\partial^2 p_a}{\partial \lambda^2}\right]. \tag{45}$$

The derivatives of pressure are estimated by means of finite differences of pressure, using the grid pattern shown in Fig. 8. Seven values of pressure are used in the computation of the derivatives at a grid point. The finite approximations to the pressure derivatives are:

$$\frac{\partial p_a}{\partial \phi} = \frac{1}{2h}(p_{a1} + p_{a2} - p_{a3} - p_{a4})$$

$$\frac{\partial p_a}{\partial \lambda} = \frac{1}{2h}(p_{a5} - p_{a6})$$

$$\frac{\partial^2 p_a}{\partial \phi^2} = \frac{1}{h^2}(2p_{a1} + 2p_{a2} + 2p_{a3} + 2p_{a4} - p_{a5} - p_{a6} - 6p_{a0})$$

$$\frac{\partial^2 p_a}{\partial \phi \partial \lambda} = \frac{1}{h^2}(p_{a1} - p_{a2} + p_{a3} - p_{a4})$$

$$\frac{\partial^2 p_a}{\partial \lambda^2} = \frac{1}{h^2}(p_{a5} + p_{a6} - 2p_{a0}). \tag{46}$$

where h is the grid spacing in radians equivalent to the 10° spacing shown in Fig. 8.

The total transport ψ, obtained by integrating the meridional component of transport (43), is:

$$\psi = \int_{\lambda}^{\lambda_0} VR\cos\phi \, d\lambda$$

$$= \int_{\lambda}^{\lambda_0} \frac{\mathrm{curl}_z \tau_S}{\beta} R\cos\phi \, d\lambda \tag{47}$$

where λ_0 is the longitude of the eastern shoreline of the ocean at latitude ϕ. The geostrophic transport ψ_g, computed by subtracting the meridional component of Ekman transport from the total meridional transport component, is given by:

$$\psi_g = \int_{\lambda}^{\lambda_0} (V - V_E) R\cos\theta \, d\lambda$$

$$= \int_{\lambda}^{\lambda_0} \left[\frac{\mathrm{curl}_z \tau_S}{\beta} + \frac{\tau_\lambda}{f}\right] R\cos\phi \, d\lambda. \tag{48}$$

Estimates of the surface stress from equations (37)–(40) are subject to considerable uncertainty. Fortunately, the magnitude of the curl of wind stress

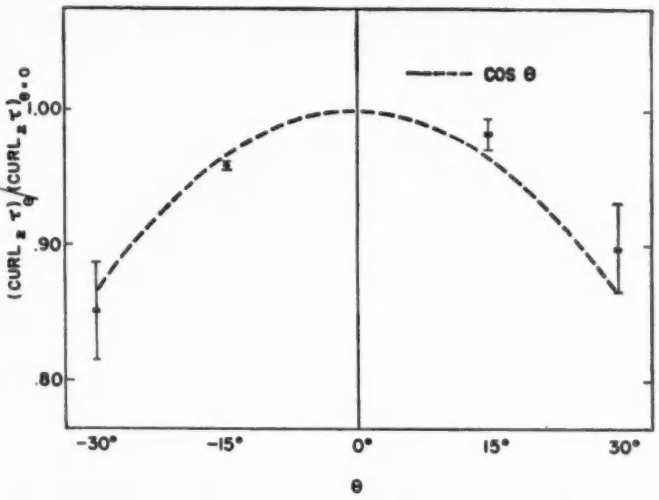

FIG. 10. Variation of the ratio of curl of wind stress for a deviation of surface from geostrophic winds of an angle θ to the curl at zero deviation. Points are averages of the ratio for several latitudes, and the vertical lines are the maximum ranges of the ratios at each angle.

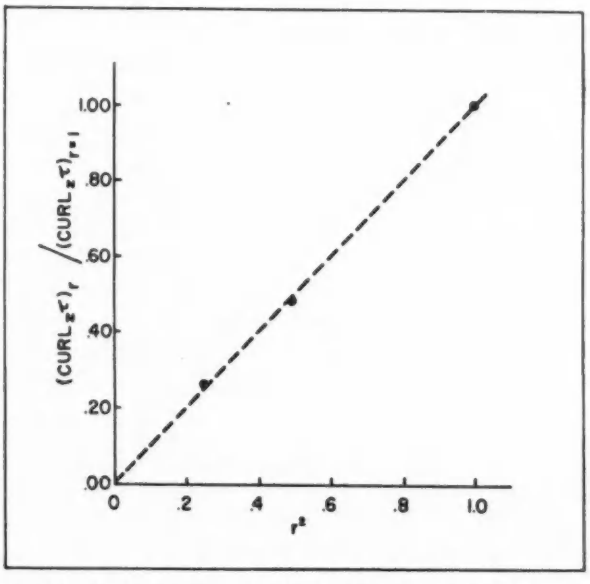

FIG. 11. Variation of the ratio of curl of wind stress with the ratio r between surface and geostrophic winds. The ratio is closely proportional to r^2.

is not critically sensitive to the angle of deviation θ of surface winds from geostrophic winds. As the stress components obey a transformation similar to (39), the curl may be written:

$$\text{curl}_z\, \tau_S = r^2 \cos\theta\, \text{curl}_z\, \tau_g - r^2 \sin\theta\, \Delta \cdot \tau_g \tag{49}$$

where τ_g is the stress vector that would be obtained if surface winds were taken equal to geostrophic winds. Thus, for small angles of deviation, the curl of wind stress is approximately proportional to $\cos\theta$ and to r^2. Computations for a given pressure field have been made for various values of θ and r and the results are shown in Fig. 10 and 11, which show that the curl of wind stress for a given value of r and θ can be scaled with reasonable accuracy to apply to any combination of r and θ within the range indicated.

A more serious error is involved in estimating the stress from the mean pressure difference. The magnitude of the stress vector depends on the square of the pressure difference between grid points, i.e.:

$$|\tau| \propto v^2 \propto (\Delta p_a)^2. \tag{50}$$

Hence, the monthly mean stress $|\bar{\tau}|$ based on estimates from daily pressure differences would be proportional to $\overline{(\Delta p_a)^2}$. However, the stress from the monthly mean pressure $|\tau_m|$ is proportional to $(\Delta \bar{p}_a)^2$. Hence, the difference between the two estimates is:

$$|\bar{\tau}| - |\tau_m| \propto \overline{(\Delta p_a)^2} - (\Delta \bar{p}_a)^2$$
$$\propto \text{variance } (\Delta p_a). \tag{51}$$

The uncertainty of the estimate of stress is of the same order of magnitude as the statistical variance of pressure difference between grid points over a period of a month. For grid points in active storm areas of the ocean, the variance could be as large as, or larger than, the mean pressure difference. Hence computed transports must be interpreted with caution.

The program is designed to output six charts giving (1) the pressure distribution, (2) the meridional and (3) zonal components of Ekman transport, (4) the meridional component of total transport and (5) the integrated total and (6) geostrophic transports. An example of each chart is shown in Fig. 12 to 17.

Short auxiliary programs have been constructed to compute averages of pressure and of each transport component. These programs have been used to compute annual and 5-year means. A subtraction program is used to obtain anomalies from the 5-year mean.

Computations for each set of monthly mean sea-level pressure distributions have been carried out for the period January 1955 to present. Each set of six charts requires about 12 minutes computing time and about 80 sets have been processed to date. The charts are published in the referred-to Manuscript Report Series of the Fisheries Research Board of Canada (Fofonoff, MS, 1960).

The calculations of transport components for each month are carried out independently of the other months. Thus, the inertia of the ocean is not taken into account. The computed transports for each month may be interpreted

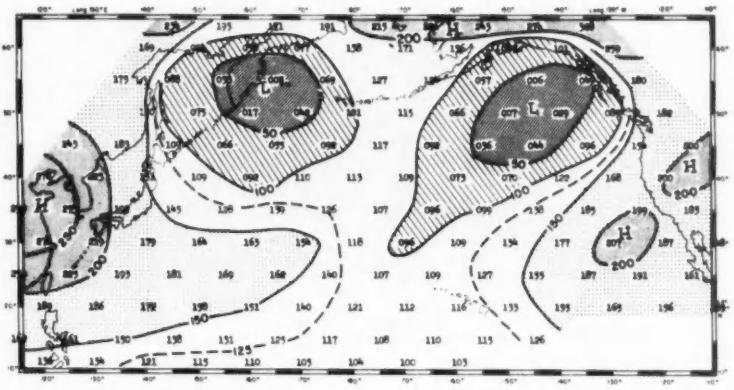

FIG. 12. Monthly mean sea-level atmospheric pressure distribution over the North Pacific Ocean, Dec. 30–Jan. 28, 1959. Pressures less 1000 mb are given in units of 0.1 mb.

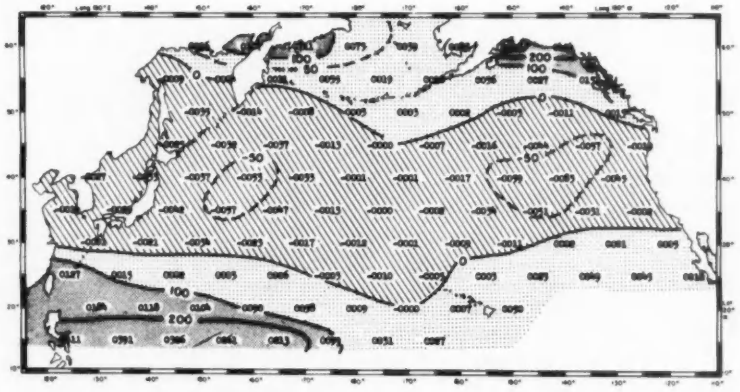

FIG. 13. Meridional component of Ekman transport, Dec. 30–Jan. 28, 1959. Positive values indicate northward movement. Values are given in units of 10 metric tons/km/sec (decimal following the last digit).

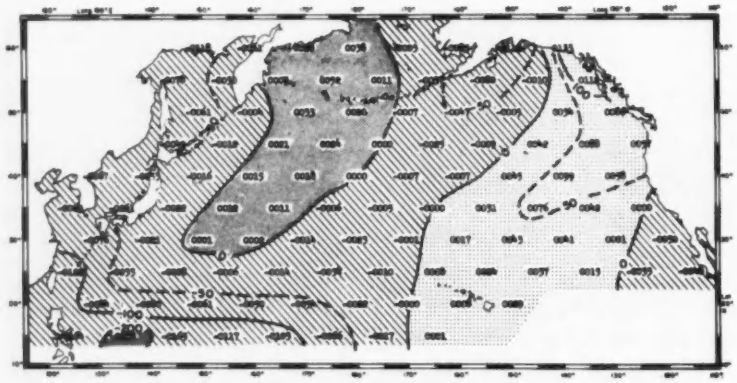

FIG. 14. Zonal component of Ekman transport, Dec. 30–Jan. 28, 1959. Positive values indicate eastward movement. Values are given in units of 10 metric tons/km/sec (decimal following the last digit).

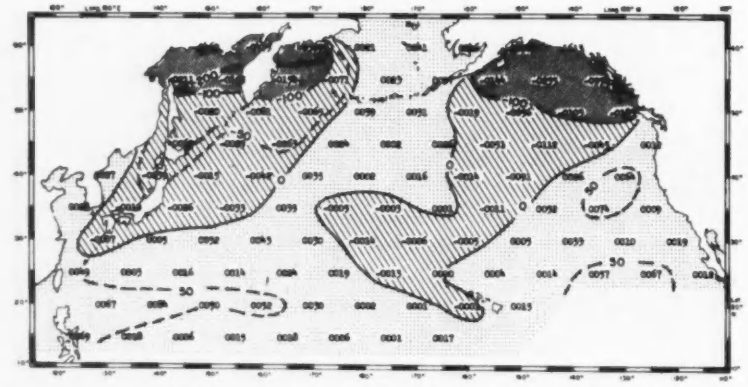

FIG. 15. Meridional component of total transport, Dec. 30–Jan. 28, 1959. Positive values indicate *southward* movement. Values are given in units of 100 metric tons/km/sec (decimal following the last digit).

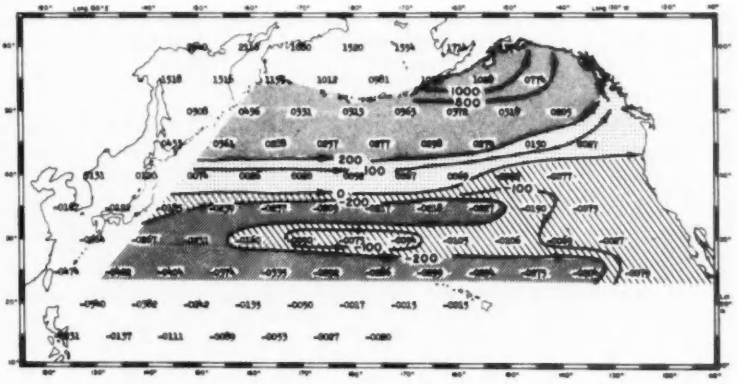

FIG. 16. Integrated total transport, Dec. 30–Jan. 28, 1959. Each value indicates the total transport between that gridpoint and the gridpoint nearest the eastern boundary of the ocean. Values are given in units of 50,000 metric tons/sec (decimal following the last digit).

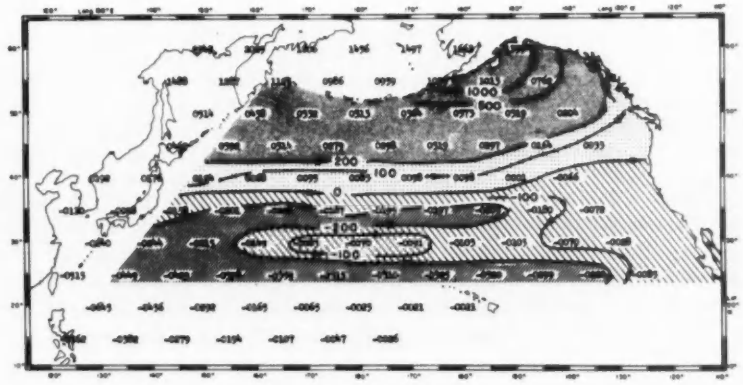

FIG. 17. Integrated geostrophic transport, Dec. 30–Jan. 28, 1959. Each value indicates the total transport less the Ekman transport between that gridpoint and the gridpoint nearest the eastern boundary of the ocean. Values are given in units 50,000 metric tons/sec (decimal following the last digit).

as the limiting flow that would occur if the pressure distribution for that month were to persist without change for an indefinitely long period of time. Alternatively, the actual transport in the ocean can be interpreted as resulting from a weighted mean of winds during a given month and a number of preceding months. It is, therefore, necessary to carry out an averaging process on the computed monthly transports to simulate the effects of inertia on the actual transport induced in the ocean.

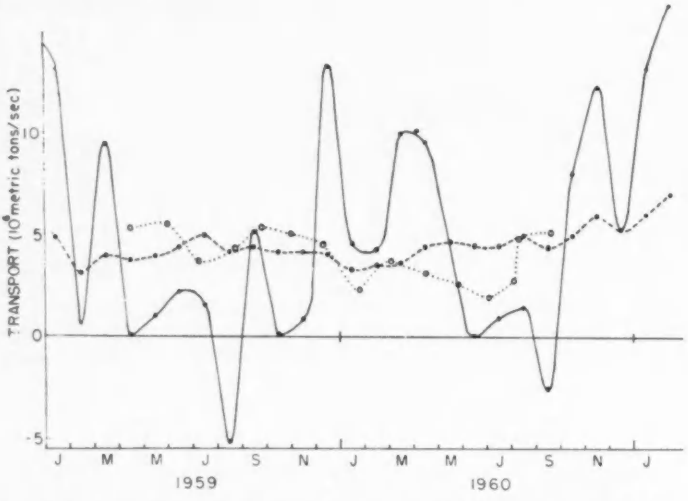

FIG. 18. Comparison of geostrophic transport (solid line) computed from monthly means of sea-level pressure with baroclinic transport relative to 1000 decibars (dotted line) obtained from oceanographic data. The broken line represents the running mean of computed geostrophic transport for the twelve preceding months. The comparison is made for a section extending from Juan de Fuca Strait to Ocean Station "P" (50°N, 145°W).

Long-term averages of computed transport should converge to the mean transport observed in the ocean within the limits of accuracy of the method. Because the numerical values of transport are highly sensitive to the proportionality factors used in relating geostrophic to surface winds and surface winds to surface stress, numerical agreement between computed and observed transports is not expected. An example of the agreement obtained between computed transport and baroclinic transport from oceanographic stations is shown in Fig. 18 for a section extending from Juan de Fuca Strait to Ocean Station "P" (50°N, 145°W). The baroclinic transport shows no marked seasonal change whereas the computed transports show a strong seasonal variation. Reasonably close agreement is obtained between baroclinic transport and a 12-month running mean of computed transports in which the seasonal cycle is suppressed. Further comparisons with baroclinic transports evaluated from oceanographic data are planned.

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A Method of Analysing a Polymodal Frequency Distribution and its Application to the Length Distribution of the Porgy, *Taius tumifrons* (T. and S.)[1]

By Syoiti Tanaka

I. METHODS OF ANALYSING A POLYMODAL FREQUENCY DISTRIBUTION

When we examine the length distribution of a sample of fish we often find distributions having two or more modes (Fig. 2). This polymodality is very fortunate for population studies, because from the length distribution alone we can often obtain a number of pieces of information.

Analysis of a polymodal distribution begins by separating it into the individual components (for example, age-groups) which correspond to each of the modes. An analysis into individual components by means of polymodality has much significance in cases where there are no other criteria to separate them. This method is available when age determination is difficult, or when an age-group is made up of several broods. Suda [12], for example, has applied this method in his examination of the fork-length distribution of the albacore, *Thunnus alalunga*.

In regard to methods of analysis, strict mathematical methods have been used in special situations. For example, in a case where there are only two components, for each of which the normal distribution is assumed and where the two variances are equal, Rao [7] has used the method of moments and method of maximum likelihood in his solution, while Preston [6] has suggested a graphical method. These solutions, however, do not apply to more general situations, and even if they *were* applicable, the computations are formidable. Leaving aside for the moment the question of mathematical strictness, if individual mean values are far enough apart that the modes are separate, we may be able to apply various approximate methods.

Earlier the present author [14] called attention to the significance of modes as a means of solving such problems, and discussed the nature of modes from various points of view. He showed that when two or more modes are present in a frequency distribution, the position of each mode may be regarded as the mean of its group, with sufficient accuracy. Even when minor modes are not distinguishable, if there are additional humps on a curve, the points of inflection of the curve are related to each individual mean.

As a matter of fact, the use of modes had already been advocated by Buchanan-Wollaston and Hodgson [2] some 20 years ago. These authors objected to

[1]Translated from Japanese by Hack Chin Kim, United States Bureau of Commercial Fisheries, Seattle; edited by S. Tanaka and W. E. Ricker. The Japanese text of this paper was published in Bulletin of the Tokai Regional Fisheries Research Laboratory, Tokyo, Japan, No. 14, pp. 1–13, 1956.

J. Fish. Res. Bd. Canada, 19(6), 1962.
Printed in Canada.

the smoothing out of 'bumpy' distributions by means of running averages even in cases where the sample size is small, and insisted that the individual humps indicate meaningful modes to which normal curves ought to be fitted. They showed that normal curves may be fitted by selecting 3 points around the mode and fitting a parabola to the logarithms of those points, but held that a 'free-hand' fitting is also adequate.

Harding [4], on the other hand, proposed a method for analysing a polymodal frequency distribution into individual components by plotting a cumulative frequency curve on probability paper, and observing the points of inflection of the curve. Cassie [3] developed that method and demonstrated simple methods of computation, using many examples. Oka [5] made use of the fact that a normal distribution becomes a parabola when logarithms are taken, but he did not fit a parabola directly to it. Utilizing the fact that the differential coefficient of a parabola forms a straight line, he proposed a method of fitting several straight lines, that slope downward to the right, to the first difference of the logarithms of the frequency distribution.

Let us summarize and compare the methods just described. The objective of Buchanan-Wollaston and Hodgson was to follow the growth of individual broods within a single age-group by the shift in the position of their modes with time, and to determine the relative size of these broods from the heights of the modes. Tanaka argued for the usefulness of such modes. But in order to estimate the composition of the individual components accurately, we must know both the height of the mode and the standard deviation of the distribution of each component, and in general it is not easy to get an accurate estimate of this standard deviation. The method of fitting a parabola to several points near the modes permits the computation of standard deviations, but the computation is troublesome and there is the further difficulty, when the points available are few, of attaining precision in estimation. In the case of 'freehand' fitting of curves, it is impossible to arrive at accurate standard deviations.

[page 2] Cassie [3], on the other hand, starting from Buchanan-Wollaston and Hodgson's concept, has analysed polymodal frequency distributions completely into normal curves, and obtained the mean and standard deviation of each group and the contribution of each to the whole distribution. Consequently, it is possible to plot growth curves using the results, and to analyse the variations in stock size from the age compositions obtained. But when this method is examined, it is readily apparent that the age composition so obtained is nothing more than a division of the total distribution by means of ordinates placed in the troughs between the modes, or near the flat part between humps. According to figures given by Tanaka ([14], Table 3), the ratio of the areas of the sections thus obtained deviate considerably from the actual representation of each component. It is possible to correct this, of course, by a method of successive approximations, but the computation is rather troublesome.

Oka's method is interesting because it has a different basis, but the use of differences involves a danger of magnifying errors in the frequency distribution. It would be difficult to expect full precision when there are few points usable for determining the position of the lines.

To sum up, it may be said that none of the above methods is perfect, in the sense of making full use of the fortunate fact that length distributions are often polymodal. The method described below, too, is merely a simple development of the method of Buchanan-Wollaston and Hodgson. Although it may be superior to other proposed methods in certain points, it resembles them in that it depends partly on good luck [in having a frequency distribution with fairly well separated modes, as in Fig. 2]. Further developments in this area of study are needed.

In carrying out this study, I received guidance in various ways from Mr Susumu Kurita of this Laboratory, for which I hereby express my deep gratitude.

II. A METHOD OF FITTING NORMAL CURVES TO A LENGTH DISTRIBUTION

Assuming that length, x, has a normal distribution in each of the individual components of a frequency distribution; and that for a given component the mean is m, standard deviation σ, and total number of individuals N; then the length distribution expected in that component becomes:

$$f(x) = \frac{N}{\sqrt{2\pi}\,\sigma} e^{-\frac{(x-m)^2}{2\sigma^2}} \tag{1}$$

Taking common logarithms, we get:

$$\begin{aligned} \log f(x) &= \log \frac{N}{\sqrt{2\pi}\,\sigma} - \frac{(x-m)^2}{2\,\sigma^2} \cdot 0.4343 \\ &= ax^2 + bx + c \end{aligned} \tag{2}$$

where: $a = -0.4343/2\sigma^2$; $b = 0.4343m/\sigma^2$

$$c = \log(N/\sqrt{2\pi}\,\sigma) - 0.4343m^2/2\sigma^2$$

Expression (2) describes a parabola.

If $m = 0$, we get $b = 0$, $c = \log(N/\sqrt{2\pi}\,\sigma)$, and so there results:

$$\begin{aligned} \log f(x) &= ax^2 + c \\ &= -\frac{0.21715}{\sigma^2} x^2 + \log \frac{N}{\sqrt{2\pi}\,\sigma} \end{aligned} \tag{3}$$

A length frequency curve can be analysed into its individual components using these relationships, by fitting several parabolas to the frequency distribution of the logarithms of the observed numbers.

The actual procedure is as follows:

i) Compute the numerical value of the curve (3) for a number of different values of σ, and draw a group of curves on translucent tracing paper of good quality. It is desirable to take the values of σ at equal intervals, and it will be well to make the interval less than 1/10, or less than 1/20 if possible, of the expected value of σ. Further, it is best to place successive curves one above the other, in order of increasing values of σ, and to space them at equal intervals at

the ordinate $x = 0$; this makes them easier to read. No grid lines are needed except the y-axis drawn at $x = 0$; in fact such lines are rather a nuisance. At least two identical copies of the graph are necessary.

ii) Keeping the scales of x and y the same as when the parabolas were drawn, we plot the frequency distribution values converted to logarithms. It is necessary that the paper be translucent. Semi-logarithmic graph paper would be convenient if available, but blank sheets may be used with lines drawn on them.

[page 3] iii) Keeping the sheet which has the distribution plotted on it in a fixed position, insert underneath it the sheets which have the parabolas drawn on them. Keeping the y-axis of the parabolas exactly vertical, move the sheet up and down, right and left, so as to adjust it to the total frequency distribution. It is best to begin first with the most conspicuous mode. Determine the most suitable value of σ, and the most suitable position for the peak of the parabola, for 3 or 4 points near the mode. When the position of one sheet is decided upon, fix it in that position and plot the frequency distribution of residuals obtained by subtracting the antilogarithms of the values indicated by the parabola from the actual frequencies. This done, the adjacent mode emerges comparatively clearly — it has been obscured up to this time because of the overlapping of the distributions of adjacent components. Next, adjust the second sheet to the adjacent mode in the same manner as before. When the parabola of the adjacent mode is determined, fix that sheet and plot on it the frequency distribution that remains when this parabola is subtracted from the total. Correct the position of the parabola that was adjusted first. Then fix the first sheet and correct the position of the second sheet. Repeat this procedure and make the sum of the two parabolas (when converted to actual numbers) fit most suitably the frequency distribution near the two modes and the valley between them. Ideally, it would be best to prepare 3 sheets with curves drawn upon them, adjust these in relation to 3 modes, and determine the position of the middle parabola. When a parabola's position is decided, copy the curve on the frequency distribution sheet, and take a reading of the position of the peak (mean value) and σ (standard deviation).

iv) Care must be taken with the following points in adjusting the parabolas.

a. The degree of discrepancy between the observed frequency f_x and the fitted curve $f(x)$ should be so marked on the logarithmic sheet as to be roughly inversely proportional to $\sqrt{f(x)}$. In other words, even if the apparent discrepancy becomes quite large where $f(x)$ is small, it is better to fit the curve closely to f_x where $f(x)$ is large. This reduces the magnitude of χ^2, which represents the goodness of fit to the frequency distribution if the latter has been obtained by simple random sampling. If the fish have been collected by a complex sampling procedure, the weight of each frequency f_x will not be uniform, but the method outlined above may safely be given general application.

b. Care must be taken to make the discrepancies between f_x and $f(x)$ come out, as far as possible, as positive and negative alternately. If a point is a long way off the curve, the points on either side of it should be considerably off in the opposite direction.

c. Where f_x is small, at either end of the length distribution of a sample, it is better to cut off some points. The weight of f_x is small in that region, in any event.

d. When both modes and humps are absent, or in other words when there is absolutely no foreknowledge of the components that make up the distribution, it is dangerous to fit parabolas by this method. Unrestricted increase of the number of components is meaningless. Remember that three degrees of freedom are lost whenever one parabola is fitted.

III. EXAMPLES AND COMPARISON WITH OTHER METHODS

Example 1. Rao's data

Let us first analyse the example used by Rao ([7], page 165) by means of the present method. The result is shown in Table 1. According to Rao's result, the distance between the means is 2.63 cm, which is only 1.45 times the standard deviation 1.82, and consequently the modes are not necessarily separate. The observed frequency distribution does not make it possible to decide definitely that it is a mixture of two groups. As compared with the maximum likelihood solution, the graphical method cannot be said to yield as good a result. But in respect to estimate of the ratio of mixture of the two groups, the difference between the methods is less than the standard error attached to the maximum likelihood estimate (see [7], page 170), and in other respects also the differences would not be serious in actual practice. If this were a bimodal distribution, more accurate estimation would of course be possible.

Example 2. Length distribution of the porgy caught by the pair-trawl fishery of the East China Sea

In the fork length distribution [8] of porgy caught by trawl fishing in the East China Sea, several very conspicuous modes and humps appear (Fig. 1 and 2), and this is one of the most suitable bodies of data to which the author's method may be applied. To this distribution I have applied the method shown in the previous section; and also, for comparison, Cassie's method utilizing probability paper, and the method of fitting a parabola by least squares as used by Buchanan-Wollaston [1]. Data from September to November 1950 were selected. The frequency distribution during this period seems to be a more typical example that that of the succeeding period. The fish were selected by a three-stage sampling method, and the number of individuals measured was 14,054.

[page 4] The following is a concrete demonstration of the steps taken in plotting the curves. Taking the interval between values of σ as 0.1 in the group of parabolas, two identical sheets were prepared. With the material used here it is best to start from the left (the youngest age-group) in fitting the parabolas. The position of the parabolas was determined almost finally after one adjustment. Frequencies under 9 cm and over 31 cm were not used; these may contain frequencies belonging to other components. The results of fitting the curves are shown in Fig. 1 and 2. When we compute χ^2 for the 22 classes from 9 cm to 31 cm,

TABLE 1 [page 4]. Analysis of Rao's [7] data by the author's method. The results of the analysis differ somewhat from those of Rao's maximum likelihood method. Two sets of the author's standard deviations are greater than Rao's, probably attributable to the effect of grouping. The value of χ^2 is extremely small. (Figures in parentheses show RAO's maximum likelihood estimates.)

Class interval *cm*	Observed frequency	Expected frequency	Group (I)	Group (II)	Difference
– 8.5	3	3.6	3.6		−0.6
8.5– 9.5	9	8.7	8.7		0.3
9.5 10.5	21	21.6	21	0.6	−0.6
10.5–11.5	40	40.2	38	2.2	−0.2
11.5–12.5	59	60.5	54	6.5	−1.5
12.5–13.5	76	74.5	60	14.5	1.5
13.5–14.5	79	77.5	53	24.5	1.5
14.5–15.5	69	67	36	31	2.
15.5–16.5	46	49	19.5	29.5	−3.
16.5–17.5	30	29.5	8	21.5	0.5
17.5–18.5	13	14.5	2.5	12	−1.5
18.5–19.5	7	5.9	0.7	5.2	1.1
19.5–	2	2.1		2.1	−0.1
Sum	454	454.6	305.0	149.6	−0.6
			(12.65)	(15.28)	
Mean, *cm*			12.93	15.33	
			(1.82)	(1.82)	χ^2=0.841
Stand. dev., *cm*			2.0	1.9	
			(56.7)	(43.3)	
Proportion, %			67.1	32.9	D.F.=7

we get 16.56. The degrees of freedom are $22 - (3 \times 5) = 7$, and the χ^2 table shows that this value is between the 2% and 5% levels of significance. The discrepancy is significant, but here it has little meaning[2].

In the method using probability paper, the cumulative relative frequency is first obtained, and this is plotted on the probability paper. The points line up in a meandering manner. Starting with a trial division of the curve into components at 46%, 74%, 91% and 97.5%, several successive corrections were made until the points for each of 5 components come very close to each of five straight lines. Computation of χ^2 for the 22 classes between 9 cm and 31 cm gives 12.41, and the level of significance is between 5% and 10%. This value of χ^2 is smaller than that obtained by fitting parabolas, but the accuracy of these two methods is of the same order. The trouble involved in this method is quite considerable, because it involves conversion to relative frequency, the opposite conversion, and the re-computation made necessary by correction of the position where the distribution is divided into two parts; [page 5] whereas in the graphical method of fitting parabolas all the computation needed is addition and subtraction on the abacus.

[2]Since there are errors attributed to the weighting of observed values connected with the method of sampling, errors attributed to the curves plotted by visual inspection, errors in reading the numerical values from the graph, and error in σ on account of the 0.1 interval, these values of χ^2 have little meaning as a test of significance.

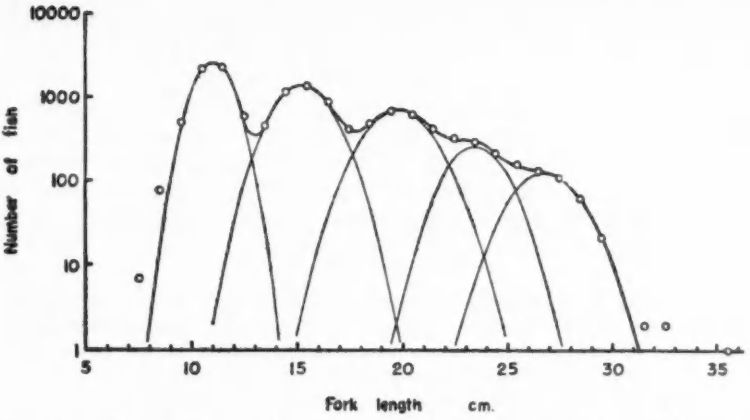

FIG. 1 [page 5]. Fork length frequency curve for porgies, on a logarithmic scale (September-November, 1950). Small circles indicate the observed frequency. Light lines are the normal curves fitted to each component age-group by the author's method, which appear as parabolas when plotted on this scale. The heavy line is the sum of the several normal curves. The total number measured was 14,054.

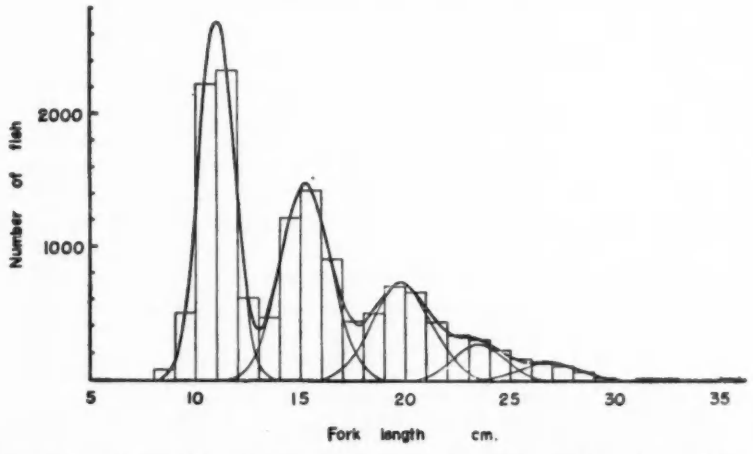

FIG. 2 [page 5]. Fork length frequency curve for porgies (same data as in Fig. 1), on an arithmetic scale. The histogram shows the observed frequencies. Light lines are the normal curves fitted to each age-group by the author's method. The heavy line is the sum of the normal curves.

In fitting parabolas by least squares, which differs from the graphical fitting in that it involves computations instead of graphs, the method of successive approximations was not used because of the troublesomeness of the computations; rather, starting from the mode at the extreme left, parabolas were fitted one after the other by taking 4 points near the modes. Because of this, the

influence of the left-hand tail of a curve on the adjacent curve to the left is not taken into account. This influence will be the greater, the greater is σ and the greater the ratio between the peak on the right side and the peak on the left side, of two adjacent components. In addition, there is the effect of the relatively small weight given to classes where the frequency is large, caused by fitting curves to logarithms with equal weight, so that, as with the two previous fittings, the sum of the values of χ^2 in the same 22 classes (9–31 cm) is more than 26.45, which far exceeds the 1% level of significance. There is absolutely no advantage to be derived from these complicated computations.

TABLE 2 [page 6]. Observed frequencies of fork length distribution of porgies during the period September-November, 1950, and the expected frequencies obtained by three methods—the author's graphical method, Cassie's probability paper method, and Buchanan-Wollaston's least squares method.

Fork length cm	Observed frequency	Expected frequency		
		Author's method	Probability paper	Least squares
7–8	7			
8–9	79	19	22	29
9–10	509	480	488	511
10–11	2240	2260	2258	2217
11–12	2341	2330	2322	2372
12–13	623	620	648	700
13–14	476	543	492	482
14–15	1230	1210	1186	1181
15–16	1439	1446	1439	1506
16–17	921	919	953	953
17–18	448	460	444	449
18–19	512	521	491	508
19–20	719	727	722	726
20–21	673	682	687	683
21–22	445	446	438	446
22–23	341	330	333	331
23–24	310	314	316	334
24–25	228	233	243	259
25–26	168	158	161	168
26–27	140	142	140	139
27–28	114	113	117	115
28–29	64	65	63	64
29–30	22	21	21	24
30–31	0	4	4	5
31–32	2	...	...	1
32–33	2			
33–34	0			
34–35	0			
35–36	1			
Total	14,054	14,043	13,988	14,203
χ^2(D.F. = 7)		16.56	12.41	27.45

TABLE 3 [page 6]. Comparison of the results obtained by three methods. A: the author's method. B: Cassie's method. C: Buchanan-Wollaston's method.

Item	Method	Age: I	II	III	IV	V
Mean *cm*	A	10.99	15.26	19.84	23.50	26.82
	B	11.02	15.33	19.85	23.46	26.92
	C	11.05	15.32	19.85	23.58	26.82
Standard deviation *cm*	A	0.8	1.2	1.4	1.2	1.4
	B	0.76	1.15	1.32	1.29	1.54
	C	0.844	1.161	1.412	1.212	1.443
Age composition numbers	A	5627	4485	2630	840	461
	B	5664	4427	2502	970	429
	C	5782	4415	2640	911	449

[page 7] A synoptic view of the results obtained by the three methods is shown in Tables 2 and 3. The three may be said to agree satisfactorily. The agreement is particularly good in respect to the mean values.

A point which causes no difficulty when probability paper is used, but which requires care when parabolas are fitted, is the fitting of a continuous function to frequencies divided into classes. In other words, it is the probability density that results in the parabola when logarithms are taken, while that which corresponds to the observed frequency in a given class interval is the integral of the probability density within that class. Consequently, whenever the standard deviation is quite small in relation to the width of a class interval, a considerable difference arises between probability density and expected frequency within a class. However, if the standard deviation is more than 1 class interval, no very great difference will occur. If it is considerably less than 1, fitting of parabolas will lose much of its meaning, because the remaining degrees of freedom vanish almost entirely and parabolas fit perfectly even meaningless humps on a frequency distribution.

It is easy to remove this effect of classification. It can be done when preparing the curves by drawing, instead of the parabola, the logarithm of the function:

$$f(x) = \frac{1}{\sqrt{2\pi}\,\sigma}\int_{x-\frac{1}{2}}^{x+\frac{1}{2}} e^{-\frac{x'^2}{2\sigma^2}}dx' = \frac{1}{\sqrt{2\pi}}\int_{t-\frac{1}{2\sigma}}^{t+\frac{1}{2\sigma}} e^{\frac{t'^2}{2}}dt' \qquad (4)$$

for various values of σ. In practice these curves fit the parabolas fairly well. However, these curves which take account of the effect of classification are inconvenient to use. They have to be made anew whenever the class division is changed (when two classes are combined into one, for example), and they become unusable when the scale of the length on the graph changes.

With parabolas, by contrast, the class division can be changed freely in the middle of the process, and even when the length scale is changed, if we convert the values of σ to the new scale, the curves first drawn can be made to serve all cases.

To compare the three methods discussed so far, as far as the example used here is concerned, the method using probability paper and the method of fitting

parabolas graphically both seem to be superior in that they make χ^2 small; but the parabola method is the simpler. In conclusion, I believe that the method of analysing polymodal distributions into their components by fitting parabolas graphically is quite satisfactory for practical purposes.

IV. ANALYSIS OF THE LENGTH DISTRIBUTION OF THE PORGY, *TAIUS TUMIFRONS* (T. AND S.)

When it became clear that the method of fitting parabolas graphically was sufficiently practical, normal curves were fitted to the fork length[3] distribution of porgy for the period September 1950 to December 1952, thus separating it into several components. Because this method, on account of its few degrees of freedom, requires samples of considerable size, [page 8] curves were fitted to the samples for periods 3 months long, divided according to fishing season, taken by the Seikai Regional Fisheries Research Laboratory. But the data for September 1951 were treated as a separate unit. Thus the whole period was divided into 10 fishing seasons. Table 4 gives a conspectus of the fishing seasons and shows the values of χ^2 indicating the goodness of fit of the frequencies that were fitted, while Table 5 shows the estimated values of the parameters by year-classes[4]. Every value of χ^2 is quite large, but as mentioned above, we need not attach too much importance to that fact.

TABLE 4 [page 7]. Goodness of fit between observed and expected frequencies. Most of the χ^2 are greater than the values for the 1% level, but they may be acceptable on the basis that there are many reasons which might increase the values of χ^2, such as the multi-stage sampling method, error of reading figures from the graph paper, etc.

Season	χ^2	D.F.	χ_0^2 (1%)
Sept. — Nov. 1950	16.56	7	18.48
Dec. 1950 — Feb. 1951	141.78	"	"
Mar. — May 1951	25.82	"	"
June — Aug. "	27.02	"	"
September "	43.27	8	20.09
Oct. — Dec. "	43.35	6	16.81
Jan. — Mar. 1952	89.67	9	21.67
April — June "	71.28	6	16.81
July — Sept. "	46.84	5	15.09
Oct. — Dec. "	21.95	"	"

Here let us touch briefly on the names to be used for the age-groups. Strictly speaking, we do not know the correct ages, because it is uncertain how old a year-class is when it appears in the catch for the first time. Further, among the small-sized fish two groups can be identified within what is a one-year cycle among the higher age-groups; these correspond to the twice-yearly spawnings mentioned by Shindo and Aoyama [11]. One of them is about 10 cm in length

[3]Porgies were measured by fork length in these data.

[4]Investigations from several points of view at the Seikai Regional Fisheries Research Laboratory have made it clear that each mode corresponds to one age-group.

when it appears in the catch at the beginning of the calendar year; the other appears in the catch at about the same length, beginning about the middle of the year. Since the difference in mean length between two adjacent groups is almost equal to a half-year's growth, it is difficult to determine on the basis of length alone which two groups should be combined as one year-class.

But if we check the length frequency distributions carefully, it will be seen that the early-1951 group (the group which was recruited in early 1951) is absorbed [page 9] into the previous group (the smallest group in the autumn of

TABLE 5 [page 8]. Results from the analysis of fork length distributions of porgy; the data are also illustrated in Fig. 3, 4 and 5.

	Year-class: 1945	1946	1947	1948	1949*s*	1949*a*	1950*s*	1950*a*	1951*s*
Mean fork length, *cm*									
Season									
(Age)	(V)	(IV)	(III)	(II)	(I)	(I)			
IX–XI, 1950	26.82	23.50	19.84	15.26	10.99				
(Age)	(VI)	(V)	(IV)	(III)	(II)	(II)	(I)	(I)	
XII, 1950–II, 1951	27.00	23.95	20.31	16.33	12.27				
III–V, 1951	...	25.73	21.52	17.37	13.35	10.17			
VI–VIII, 1951	...	27.81	22.44	18.37	14.35	11.77	8.94		
IX, 1951	...	28.12	23.64	19.57	15.10	...	9.83		
X–XII, 1951	...	27.57	24.01	19.77	15.59	...	12.11		
(Age)		(VI)	(V)	(IV)	(III)	(III)	(II)	(II)	(I)
I–III, 1952	...	...	26.40	20.75	16.50	...	11.67		
IV–VI, 1952	...	...	26.06	21.57	17.63	...	13.10	11.14	
VII–IX, 1952	...	30.59	26.10	22.33	18.10	...	14.37	11.85	8.97
X–XII, 1952	...	...	...	24.18	19.90	...	15.57	13.60	10.93
Standard deviation in length, *cm*									
(Age)	(V)	(IV)	(III)	(II)	(I)	(I)			
IX–XI, 1950	1.4	1.2	1.4	1.2	0.8				
(Age)	(VI)	(V)	(IV)	(III)	(II)	(II)	(I)	(I)	
XII, 1950–II, 1951	1.5	1.4	1.3	1.2	1.3				
III–V, 1951	...	1.7	1.5	1.2	1.0	1.0			
VI–VIII, 1951	...	1.6	1.7	1.3	0.9	0.9	0.9		
IX, 1951	...	1.3	1.4	1.2	1.1	...	1.4		
X–XII, 1951	...	1.3	1.5	1.2	1.1	...	0.9		
(Age)		(VI)	(V)	(IV)	(III)	(III)	(II)	(II)	(I)
I–III, 1952	...	...	1.7	1.7	1.2	...	0.9		
IV–VI, 1952	...	...	1.7	1.5	1.2	...	0.8	0.8	
VIII–IX, 1952	...	1.6	1.6	1.7	1.6	...	1.0	0.8	0.7
X–XII, 1952	...	...	...	1.7	1.7	...	0.8	0.8	0.8
Estimated number in catch, *millions*									
(Age)	(V)	(IV)	(III)	(II)	(I)	(I)			
IX–XI, 1950	0.46	0.84	2.63	4.48	5.63				
(Age)	(VI)	(V)	(IV)	(III)	(II)	(II)	(I)	(I)	
XII, 1950–II, 1951	0.36	0.49	0.85	1.98	9.11				
III–V, 1951	...	0.39	0.77	2.29	6.18	0.15			
VI–VIII, 1951	...	0.13	0.52	0.97	2.89	1.11	0.31		
IX, 1951	...	0.03	0.09	0.45	1.82	...	1.88		
X–XII, 1951	...	0.25	0.53	2.33	2.32	...	0.56		
(Age)		(VI)	(V)	(IV)	(III)	(III)	(II)	(II)	(I)
I–III, 1952	...	...	0.33	0.83	7.06	...	2.67		
IV–VI, 1952	...	...	0.20	0.35	2.36	...	2.48	3.30	
VII–IX, 1952	...	0.01	0.14	0.50	1.65	...	1.44	0.54	0.62
X–XII, 1952	...	...	...	0.61	1.43	...	1.42	1.66	2.50

1950), and that the middle-1951 group pairs up with the early-1952 group. Therefore it may be concluded that the middle group of one year and the early group of the following year belong to the same year-class; perhaps the former is the spring (*s*) group spawned in the year previous to recruitment, and the latter is the autumn (*a*) group spawned the year before that. On this basis, the age when the fish are first caught is 1-year-old for the *s*-group and 2-years-old for the *a*-group (the *s*-group which joins this latter group being also 2-years-old at that time). Even if this identification be wrong, it would not affect the later argument greatly.

The principal age-groups which constitute the stock are 1-year-olds to 5-year-olds, but in addition a few quite small fish are seen, apparently less than 1 year of age, and also large fish (nearly 35 cm) of perhaps 6 years or older. In general, fish of this species begin to be caught about a year and a half after hatching, continue to be caught until the end of the year they are age 5, and then diminish suddenly.

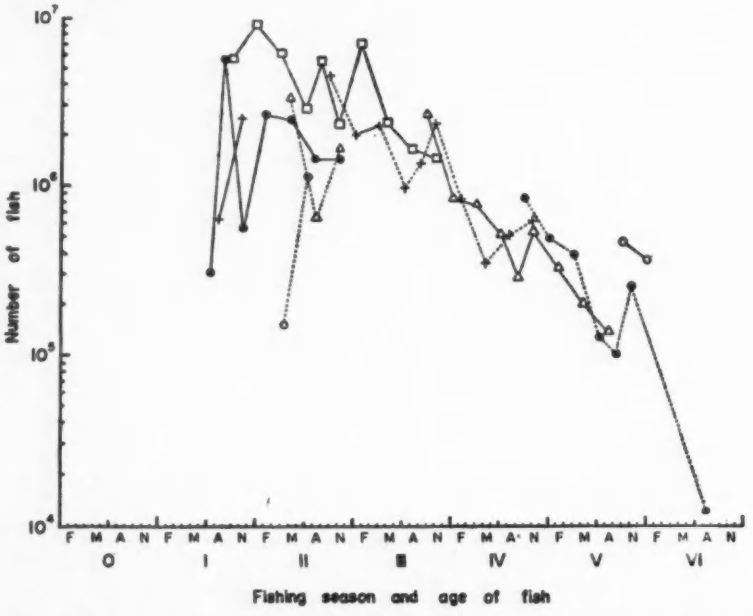

FIG. 3 [page 9]. Estimated numbers of porgies in the catch at quarter-year intervals, grouped by year-classes (for identification see Fig. 4). Yearly survival rate is estimated as about 0.3 after age I; it appears that year-class strengths were poorer in 1949 and subsequently than they were in the preceding years.

When we plot the number of fish in individual year-classes against age, we get Fig. 3. The fluctuation in the catch by season is very great, and the materials used were samples for only 2 years and 4 months, so that from these data alone

it is difficult to discuss fluctuations in stock size. In general, both the spring-group and the autumn-group complete their recruitment into the exploited stock while they are age 2, and begin to decrease in number sharply after that age. As regards the annual decrease after age 3 is reached, although we do not have accurate figures, the rate of annual decrease is about 0.7 [instantaneous rate = 1.2] when all year-classes are considered together. A rate of about the same order is obtained when the year-classes are considered separately.

It is not clear whether year-class fluctuations occur. For the year-classes from 1946 through 1949 abundance seems to be about the same, but the 1945 year-class lies above the others, and the points for the 1950 and later year-classes (combining spring and autumn groups) are down. If it is actually true that the strength of the year-classes has declined since 1950, it indicates that the porgy stock is in a dangerous condition.

In analysing age composition, the amount of effort should also, naturally, be taken into consideration, but we will not go into that here.

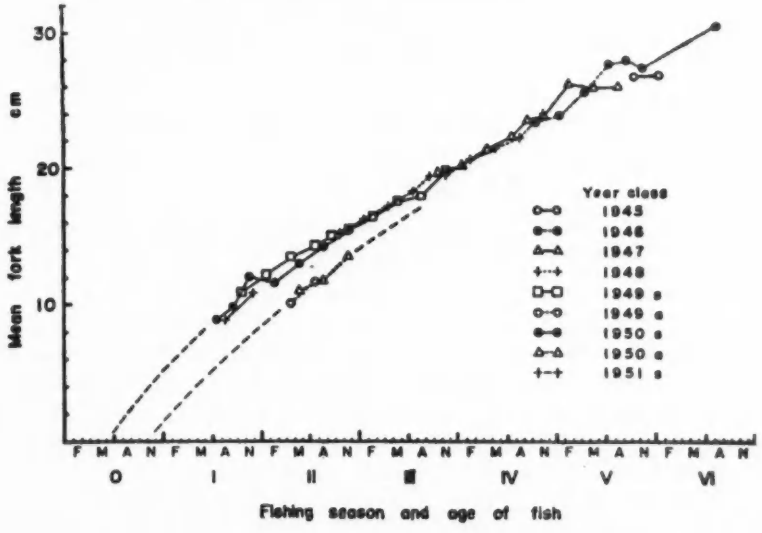

FIG. 4 [page 10]. Mean fork length of porgies, by year-classes. An approximate growth curve is obtained from the increase in mean length. Broken lines show estimated growth curves prior to the appearance of the fish in the commercial landings. The letters *s* and *a*, appended to year-classes, indicate the spring brood and autumn brood respectively.

Figure 4 shows mean length by year-classes plotted against age. Apart from some slight deviations among the oldest fish and the young, the points lie along an almost perfectly straight line. The following reasons may account for the deviation of the points for the 5-year-old and the 1- and 2-year-old fish.

In the case of the 5-year-olds, the precision of estimation is poor because of their scarcity and because some fish more than 5 years of age are mixed in with them. In the case of the 1- and 2-year-old fish, it can be expected that complications arise from the effect of mesh selectivity and from the mixture of the spring- and autumn-groups.

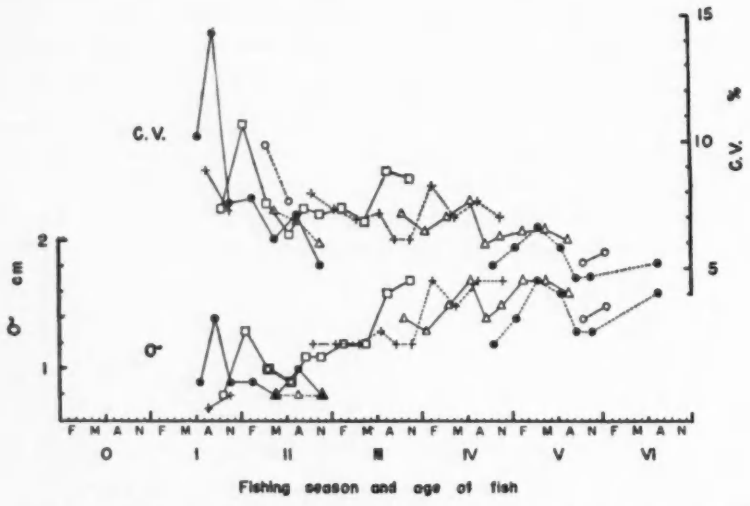

FIG. 5 [page 10]. Standard deviation (σ) and coefficient of variation (C.V.) in fork length of porgies, by year-classes. Note that standard deviation increases with age, while the coefficient of variation decreases. Year-classes as in Fig. 4.

As for the disappearance of the autumn-group after their third year, we know nothing concerning the 1950 and later year-classes because of lack of data. [page 11] In the 1949 year-class, the spring-group was so predominant that the autumn-group may have become absorbed into it so as to be no longer distinguishable. When this occurs, the mean of the mixed group approximates closely to the mean of the predominant group[5].

On the basis of the foregoing discussion, the following statement may be made concerning the growth of the porgy. Growth in length after recruitment into the fishable stock is slightly curved at one year of age, but later is very close to a straight line; the annual increase is about 4.0 cm. No seasonal fluctuation in growth rate can be detected; rather, growth seems to be uniform throughout the year. No differences are apparent between year-classes in respect to rate of growth.

Growth before recruitment to the catchable stock cannot be discussed here. However, as mentioned in the definition of ages (page 1152), the fish appear to grow to about 10 cm long during the year-and-a-half after hatching.

[5]Cf. Tanaka [14].

Figure 5 shows the standard deviation in length[6], depicted in the same way as the mean lengths of Fig. 4. It shows a tendency to increase linearly with the age. The wide dispersion of dots indicates low precision in the estimates of standard deviation. Figure 5 also shows the coefficient of variation obtained by dividing the standard deviation by the mean length. This coefficient tends to decrease as the fish become older.

Fortunately, with porgies it is possible to determine age from the scales. The data obtained by age determination can also be put to use. Consequently, population analysis by length distribution only is not enough. Some of the views presented here will doubtless be corrected when a comprehensive study is made, combining all available data. But anything more than has been presented here would exceed the purpose of this paper, so the author would like to leave it for some later occasion.

V. A NOTE CONCERNING TAKING SUB-SAMPLES FOR AGE DETERMINATION

After examining the precision of estimating age composition using length for stratification, the author earlier [13] showed that the method is quite effective for fish that make good annual growth and have only a little overlap in the range of length between ages. When a length distribution is polymodal, with one mode to each age, these conditions are fulfilled. Consequently, in the case of the porgy this will be a very promising method: that is, the age of the fish can be determined from rather small sub-samples selected from the large samples used for length measurements, and the age distribution then estimated using length for stratification. Using the data of the previous section, it is possible to estimate the precision which would be obtainable using various sampling ratios of the sub-sample.

Let us assume that the fraction of a-year-old fish in the catch is p_a, that of the ith length class is p_i, and the fraction of a-year-old fish within the ith length class is p_{ai}. Then if we measure the length of L fish in the primary sample taken from the total catch, and if we examine the age of n fish selected at random from these L, the variance in the entire catch (σ^2) and the variances within (σ_w^2) and between (σ_b^2) the length strata will be:

$$\left.\begin{aligned} \sigma^2 &= p_a - {p_a}^2 \\ {\sigma_w}^2 &= \Sigma p_i \, (p_{ai} - {p_{ai}}^2) \\ {\sigma_b}^2 &= \sigma^2 - {\sigma_w}^2 = \Sigma p_i \, (p_{ai} - p_a)^2 \end{aligned}\right\} \quad (5)$$

The precision of the age composition is:

$$V\,(p_a'') = \frac{\sigma^2}{n} - \left(\frac{1}{n} - \frac{1}{L}\right){\sigma_b}^2 \quad (6)$$

[6]The values were obtained from a 3-month distribution, and the growth during that period is about 1 cm, so that the standard deviation at a given moment is probably a little less than that shown.

The magnitude of σ_b^2/σ_w^2 becomes an index showing the effectiveness of the stratification, larger values indicating greater effect. In the examples used in the author's earlier paper [13], this value was approximately 0.5 for sardines, so that scarcely any effect of the stratification is manifest. For anchovies, on the other hand, this ratio was about 2, so that the stratification had considerable effect in improving the accuracy of the estimated age composition. This value is even greater among porgy, where it is nearly always greater than 2, usually about 4[7]. Length stratification for the estimation of age composition is extremely efficient. The most appropriate sampling fraction for the sub-sample becomes:

$$n/L = \sqrt{k_1}\sigma_w/\sqrt{k_2}\sigma_b$$

where k_1 and k_2 represent the cost of measuring length and of determining age, respectively. Remembering that k_1 is much less than k_2, we find that the number of fish used for age determination need only be quite small relative to the number measured.

VI. SUMMARY [page 12]

1) By utilizing the fact that normal frequency distributions become parabolas when logarithms are taken, a simple graphical method has been devised for analysing polymodal distributions into their components. Briefly, the method consists of (a) plotting the observed frequencies on semi-log paper; (b) drawing on transparent paper the parabolas corresponding to a series of values of σ (2 or 3 copies); (c) fitting these parabolas to the observed frequency distribution.

2) As an example, Rao's data were treated in this way, and the result compared what he obtained by the maximum likelihood method. Though the results do not coincide quite perfectly, there seems to be adequate agreement.

3) For a second example the length distribution of the porgy was analysed in this way and compared with what is obtained by (1) using probability graph paper, and (2) fitting parabolas by least squares. The method proposed here is less cumbersome than either of these and it yields good results.

4) Using the graphical method, the length distributions of porgy were analysed using the data from September 1950 to December 1952, and the age composition, mean fork length and standard deviation in length were obtained for the separate year-classes. The annual rate of decrease is about 0.7, and the abundance of recent year-classes seems to have declined. Growth in length is linear and amounts to about 4.0 cm per year. The standard deviation in length increases with age, while the coefficient of variation decreases.

5) The effectiveness of stratification by length for estimating age distribution has been examined. The ratio of the variance between strata to the variance within strata is about 4, hence stratification by length is expected to be extremely efficient.

[7]This index is greatly affected by the age composition at the time, and so we cannot think in terms of a fixed value. Generally this value is high for predominant age groups and low for weaker age groups.

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NOTES

Observations on the Morphology and Optical Properties of the Adipose Eyelid of Fishes

The adipose eyelid is a clear, fleshy structure overlying all or part of the eye in some groups of non-benthic fishes. Typically, it is almost completely divided into anterior and posterior parts by an elliptical aperture over the pupil of the eye, as is the case among the herring-like isospondyls (Clupeoidea), and the mullets (Mugilidae), jacks (Carangidae) and the mackerels (Scombridae) among the percomorphs. The ten-pounders (Elopidae) and anchovies (Engraulidae) of the isospondyls and the butterfishes (Stromateidae) and threadfins (Polynemidae) among the percomorphs lack the aperture. In the bonefishes (Albulidae) there is a very small aperture, less in vertical extent than the diameter of the pupil. The salmonoid families show a reduced form of the clupeid type of adipose eyelid, with only a small portion of the posterior part of the adipose eyelid overlying the eye.

Preliminary investigations of the optical properties of the adipose eyelid have led to the discovery that the tissue composing the structure is strongly birefringent. That is, it has different refractive indices for light polarized in mutually perpendicular planes. In addition, the amount of light absorbed by the adipose eyelid varies with the plane of polarization of the light.

The material used for this work came from living Pacific herring, *Clupea pallasii*, obtained from Howe Sound, British Columbia. Fresh mounts of adipose eyelid tissue were examined under low magnification with a microscope equipped with a rotatable polarizing filter beneath the stage. Changes in light transmission as the polarizer was rotated were noted visually and then measured by means of a photometer cell fitted to the ocular of the microscope.

A Leitz polarizing microscope of the type used in crystallographic studies was also used permitting a more accurate determination of the axes of birefringence of the material.

Initial observations indicated that the adipose eyelid transmitted less light when the plane of polarization (electric vector) was parallel with the dorsoventral axis of the adipose eyelid. The drop in transmittance at this orientation was 40 percent when compared with the transmittance of light polarized parallel with the anterior–posterior axis of the adipose eyelid.

Observations made with the polarizing microscope showed that this transmittance drop coincided with the γ (slow) axis of transmission. That is, light polarized in a plane parallel with this axis would be retarded more while passing through the tissue than light polarized in any other plane. The α (fast) axis of transmission corresponded to the anterior–posterior axis of the adipose eyelid.

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The tissue of the adipose eyelid appears as a dense structure of parallel fibers when viewed under polarized light. The fibers are oriented parallel with the dorsoventral axis of the adipose eyelid, and thus are optically positive. The structure is finer and more uniform in the portions of the adipose eyelid which overlap the eye than in the parts extending onto the cheek and snout. In the latter parts, the fibers become more diffuse, and there are isotropic areas. Sectioning the adipose eyelid in different planes showed that it tends to become isotropic when light is transmitted through it in any axis other than the distal–medial axis. That is, the birefringence is uniaxial in nature.

These results suggest that the adipose eyelid may affect vision in those fishes which possess it. Two possibilities seem apparent. First, the structure may act as a lens, increasing the focusing power of the eye. Second, it may provide a means by which the fish can detect polarized light, at least in the peripheral areas of vision. The biological significance of the latter is unknown, but the possibilities are intriguing. Further investigation is in progress.

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Amphipods in Low-Oxygen Marine Waters Adjacent to a Sulphite Pulp Mill

An oceanographic–pollution survey was carried out in waters near Prince Rupert, British Columbia, with the survey ship CHS *Ehkoli*, during the period September 13–18, 1961, to investigate the effects of industrial wastes on the marine environment.

Fern Passage, Morse Basin, Wainwright Basin and Porpoise Harbour are a series of partially-enclosed embayments connected by constricted turbulent passages, which separate Kaien and Ridley Islands from the mainland of British Columbia. A sulphite pulp mill on Watson Island discharges its effluent into Wainwright Basin by way of a small channel separating Watson Island and the mainland (Fig. 1). A cannery and reduction plant are located at Port Edward, about a half mile south of the pulp mill, and discharge a small amount of organic wastes seasonally into Porpoise Harbour.

The intertidal range in the open waters of the Prince Rupert area is relatively large, about 25 ft (7.5 m) on spring tides. The narrow channels leading to the "inside" basins retard the interchange of water so that the tidal range in Morse Basin is only a little more than 0.7 of that in Prince Rupert Harbour. Tidal currents in Zanardi and Galloway Rapids are often greater than 5 knots and may reach 10 knots or more on spring tides.

Because of the intensive tidal turbulence through the connecting passages, Porpoise Harbour and Wainwright Basin are oceanographically characteristic of well-mixed embayments. The intrusion of fairly saline water from Chatham Sound occurs near the bottom through Porpoise Channel. Complete mixing of water vertically and horizontally takes place in Zanardi Rapids, so that water at the north end of Porpoise Harbour is quite homogeneous, especially on the ebb tide.

Routine determinations of salinity, temperature, and dissolved oxygen were made by usual oceanographic methods. In addition, pH, alkalinity and concentrations of spent sulphite liquor were determined. Bottom samples were collected with a Dietz-LaFond clamshell-type snapper for characterization of bottom materials and for incidental capture of bottom organisms.

The physical and chemical characteristics of the waters at Station P14 near the north end of Porpoise Harbour, observed during the September 1961 survey, are given in Table I. Comparatively uniform salinity from top to bottom was typical for all stations occupied in Porpoise Harbour. One of the unusual features was the low dissolved oxygen concentration at all depths except near bottom, which prevailed on stations from P9 to P18. This oxygen deficiency can be attributed to decomposition of spent sulphite liquor present in fairly high concentrations in the waters of both Wainwright Basin and Porpoise Harbour (Table I). Meteorological conditions prevailing during the summer preceding the survey, i.e. a sustained period of warm, dry weather, probably aggravated the acute pollutional characteristics noted in the water.

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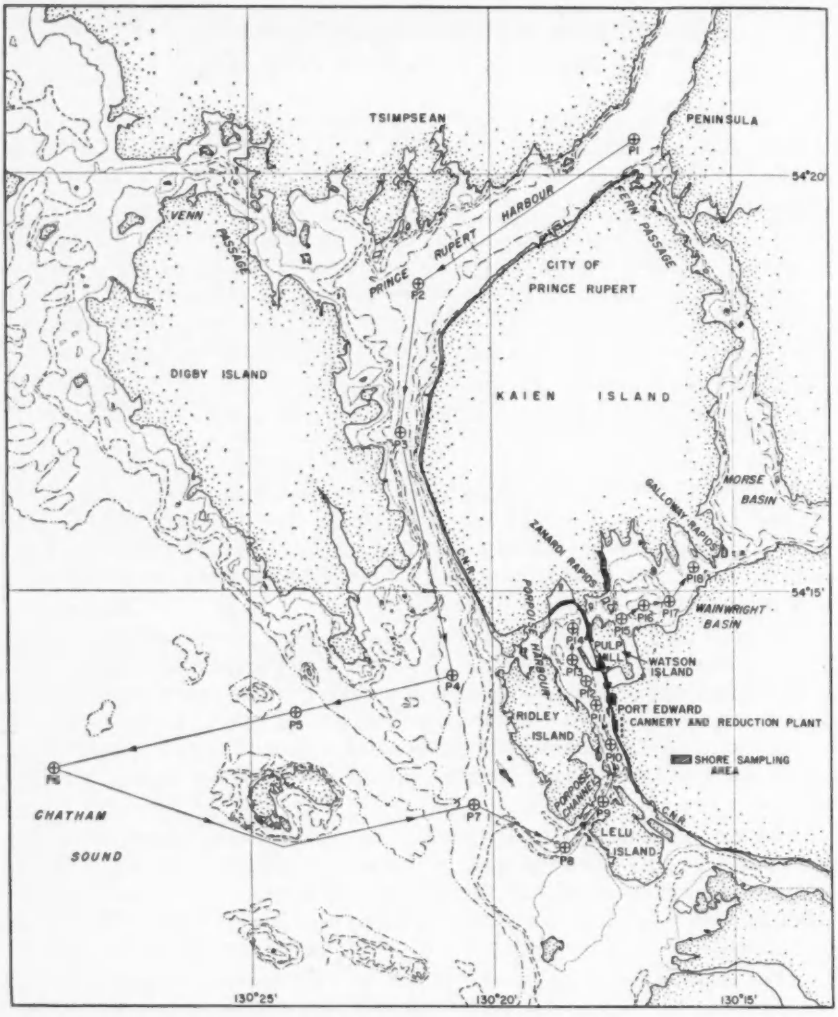

FIG. 1. Chart of waters in the Prince Rupert area, showing location of stations occupied in the survey, September 15–18, 1961.

Incidental observations were made on the flora and fauna of Porpoise Harbour and Wainwright Basin. At one time, Porpoise Harbour was evidently quite rich faunistically. Shell remains of many species of invertebrates were found in qualitative bottom sampling and intertidal collections during the survey. There were large numbers of amphipods in bottom samples at most stations within Porpoise Harbour, and many were taken by bucket from the surface at P14 while the ship was anchored for current measurements. Depths

TABLE I. Physical and chemical characteristics of the water and bottom at Station P14 in Porpoise Harbour.

Station: P14 Lat: 54°14.59′N Secchi disc: 3 ft (1 m)
Time: 1512 PST Long: 130°18.40′W Water colour: Dark brown
Date: 16/IX/61 Depth: 79 ft (24 m) Tide: Rising, near HHW
Bottom: Black mud; stones; gravel; wood chips and bark; shell; rich in decomposed organic material.

Depth (*m*)	Temperature (°*C*)	Salinity (‰)	Density σ_t	Dissolved oxygen		pH	Alkalinity		Spent sulphite liquor (*ppm*)
				(*mg/l*)	% *sat.*		Total (*meq/l*)	Carbonate (*meq/l*)	
0	12.10	27.34	20.68	0.86	9.4	7.26	1.99	1.99	176
2	11.89	27.37	20.73	0.60	6.5	7.25	1.97	1.97	109
4	11.90	27.48	20.82	0.30	3.3	7.20	1.98	1.98	179
6	11.90	27.56	20.89	0.04	0.4	7.14	1.97	1.97	208
10	11.69	27.76	21.07	0.54	5.4	7.24	1.98	1.98	178
15	11.57	28.02	21.28	1.10	11.9	7.32	2.02	2.02	150
20	11.35	28.68	21.68	2.89	32.6	7.52	2.04	2.03	79

ranged from 8–12 fathoms (15–22 m) at stations where amphipods were taken in bottom samples. Amphipods were found crawling on branches, bark fragments and chips brought to the surface from the sea bottom. Their presence in profuse abundance at and near the water surface could be easily seen from the deck of the survey ship under calm conditions. Many specimens were observed making their characteristic flicking movements as they swam towards the surface, perhaps seeking higher dissolved oxygen concentrations. Although no plankton tows were made, one bucket sample dipped from the surface of the water at P14 yielded as many as 40 specimens. Amphipods taken at the bottom were identified mainly as *Anisogammarus pugettensis* Dana. There was also a specimen of the isopod *Synidotea* sp. in one of the bottom samples. Amphipods taken at the surface were mostly *Allorchestes angustus* Dana, although there were also a number of *Anisogammarus pugettensis*.

The amphipods found in Porpoise Harbour are fairly common inshore forms of the North American Pacific coast. *A. pugettensis* is found usually in cold, slightly brackish waters. *A. angustus* is more common in somewhat shallow, warmer, brackish bays and estuaries, among *Phyllospadix* and *Zostera*. *A. pugettensis* has been found in relatively stagnant water in mud, dead algal masses and dead eel grass in the Queen Charlotte Islands. However, they have not been previously reported as being associated with polluted and/or low oxygen waters.

Pelagic amphipods, both gammarids and hyperiids, have been collected from the deeper levels of a scattering layer in Saanich Inlet, on the southeast coast of Vancouver Island. They were in the low-oxygen water of an oxycline with which the layer seems to be associated (Dr B. M. Bary, private communication).

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Range Extensions for Two Species of Caridean Shrimps (Order Decapoda) from the Northeastern Pacific

During the fall of 1960, seven species of shrimp were taken off central Oregon during an exploratory cruise of the M/V *John N. Cobb*. Included in the catches were *Pandalus jordani*, *P. stenolepsis*, *Crangon communis*, *C. resima*, *Spirontocaris holmesi*, *S. lamellicornis*, and *Eualus barbatus*. Of these species, *Crangon resima* and *Eualus barbatus* have not been previously reported off Oregon.

Crangon resima Rathbun has been reported to occur from Cordell Bank northwest of San Francisco to San Domingo Point, Baja, California in 15–266 fathoms (Goodwin, 1952a, 1952b). The occurrence of this species at the south end of Hecata Bank (Lat. 43° 59.7′, Long. 124° 32.2′) extends the recorded geographic range approximately 350 miles northward. Eight specimens were taken in the area in 60–90 fathoms.

Rathbun (1904) and Holthuis (1947) record the geographic range of *Eualus barbatus* Rathbun as Pribilof Islands to Strait of Juan de Fuca in 45–277 fathoms The occurrence of this species on the south end of Hecata Bank extends the recorded range 275 miles southward. Five specimens were taken in 60–90 fathoms.

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Egg Masses and Early Developmental Stages of the Scorpaenid Fish, *Sebastolobus*

During the spring of 1961–62 large gelatinous masses of teleost eggs were observed floating in the surface waters off the Oregon coast. As no mention of the occurrence of these unusual egg masses in the northeastern Pacific Ocean could be found in the literature, their identity was of interest.

The egg masses were of variable shape and size. They were usually bilobed, each lobe being from about 6 inches to 2 feet in length and consisting of a hollow conical sheath containing a single layer of eggs imbedded in a gelatinous matrix. These egg "balloons" were transparent: they were never seen at sea during the day, but were only observed after dark while using overhead or underwater night-lights.

Four egg masses were collected (see Table I for date and location). Three of these were preserved at sea, the other was reared in an aquarium ashore.

TABLE I. Data on the collection of the pelagic egg masses off Oregon.

Date	Location
March 30, 1961	43° 20.5′N, 124° 43.1′W
April 24, 1961	44° 00.0′N, 125° 15.7′W
May 24, 1961	44° 38.9′N, 124° 53.0′W
April 12, 1962	44° 38.0′N, 125° 15.5′W

The individual eggs of all egg masses were similar. They were 1.2–1.4 mm in diameter, each with a yellowish oil globule of about 0.2 mm diameter and a distinct perivitelline space (Fig. 1). The yolksac appeared globular in texture, turning white and translucent after preservation.

No structure could be discerned within the clear gelatinous matrix between the eggs. Eggs rotated freely within this substance (which had a consistency about like the albumen from chicken eggs) so that the eggs floated with the oil globule uppermost and the embryo, with its higher specific gravity, lowermost.

Circumstantial evidence for the identity of these peculiar egg masses was provided by the examination of fishes collected by otter trawling. On April 19, 1962, several *Sebastolobus altivelis* and *S. alascanus* (Scorpaenidae) were collected at 350–400 fathoms, 38–41 miles off the Oregon coast, including a ripe male and female *S. altivelis*. When the body cavity of the female (length, 28.5 cm) was opened, a clear elastic, mucous-like substance containing the eggs was found which hung down several times the length of the fish. Microscopic examination of these eggs, though not completely mature, revealed that they had the same basic characteristics of those from the pelagic egg masses: a diameter of 1.2–1.3 mm, oil globule of about 0.2 mm, and a distinct perivitelline space. These similarities thus indicate that the egg masses found off Oregon are produced by *Sebastolobus*.

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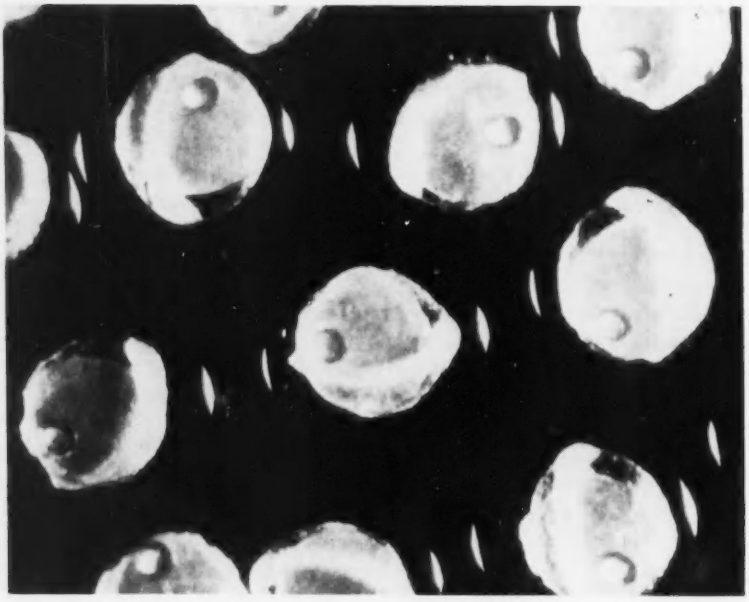

FIG. 1. Individual eggs within the egg mass. Note oil globule and perivitelline space.

OBSERVATIONS ON DEVELOPMENT

One egg mass, collected on April 12, 1962, was kept in sea water and returned to the laboratory where it was incubated in a cold room at 10°C. Observations on this collection at regular intervals furnished some information on the development of early stages.

Eggs examined one day after collecting the egg mass were found to have advanced embryos with 9–12 somites and well developed optic and otic capsules. A large Kupffer's vesicle in the tail region was noted at this time. No pigmentation was present on the embryo, whose body axis occupied about one-half the circumference of the yolksac.

One day later, somites were observed along most of the body axis with the exception of the tail region, and the lenses of the eyes were discernible.

Four days after collecting, the head and tail of the embryos were free from the yolksac. After 10 days of incubation in the laboratory, and just prior to hatching, the embryos had large median finfolds, and their bodies extended the full circumference of the yolksac, which was now only about one-half its original size. The first pigmentation was apparent at this time. Thin melanic streaks were present on the posterior part of the body midway between the end of the tail and the anus, particularly at the base of the ventral finfold. Several less distinct melanophores sometime occurred in the region of the hindgut and posterior portion of the yolksac.

The transparent prolarvae, or larvae with yolksacs, were about 2.6 mm long just after hatching. The large yolksac extended about 40% of the total length, or from the snout to the termination of the gut. Finfolds were well developed and inflated; the dorsal median finfold had a granular appearance along its dorsal margin. The finfolds were slightly indented prior to the tail. Body pigmentation was similar to that of the late embryos. The eyes were not completely pigmented.

Figure 2 shows a larva several days after hatching (length 3.0 mm). At this stage the pectoral fin lobes, located above the yolksac, were noted free from the body. The characteristic black pigmentation on the posterior part of the body was very distinct; all larvae had melanophores localized along the ventral side of somites in this region; others had melanophores dorsal to the somites in this area. Scattered melanophores are also present along the hindgut.

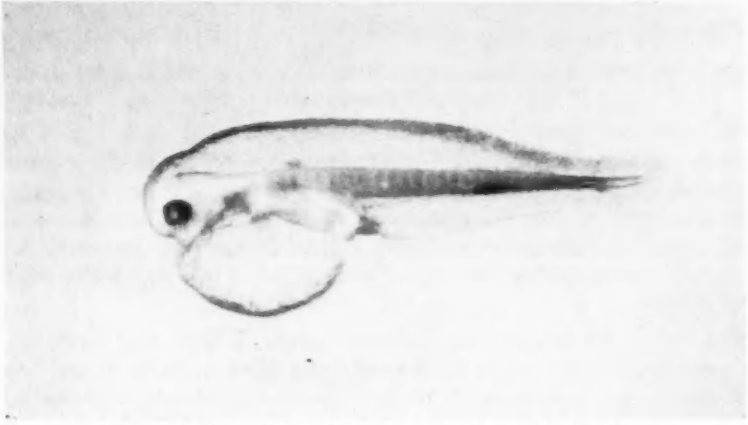

FIG. 2. Prolarva 3.0 mm in length, several days after hatching.

Within 10 days after hatching, the mouth was open and the eyes were fully pigmented. Three weeks after the first embryos hatched, the larvae averaged 3.5 mm in length (Fig. 3). The basic pattern of pigmentation, though denser and visible without a microscope, was unchanged; sometimes the melanophores on the posterior part of the body were expanded to form a complete band around the somites. No larvae were kept alive after the yolksac was reduced in size.

The specific gravity of both live eggs and larvae was less than that of sea water (at 33‰ and 10°C). When aeration of the aquarium and associated turbulence ceased, the larvae floated to the surface (with or without overhead illumination) indicating that larvae may also occur near the surface of the sea.

DISCUSSION

Two species of *Sebastolobus*, *S. altivelis* and *S. alascanus*, are found along the Pacific coast of North America, ranging from southern California to Alaska (Phillips, 1957). The life histories of these species, as well as many other fishes

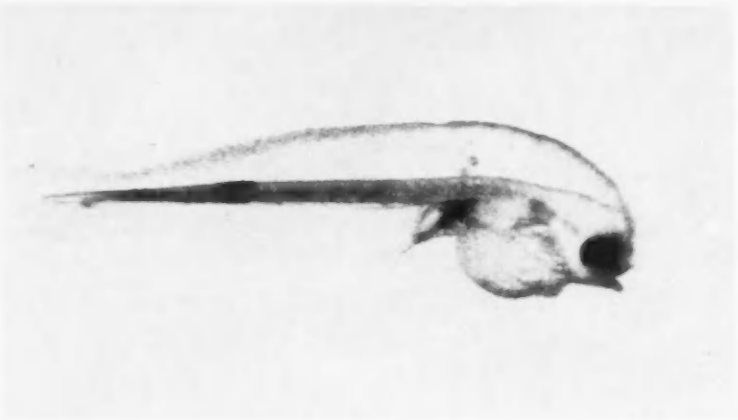

FIG. 3. Prolarva 3.5 mm in length, about three weeks after hatching, showing characteristic pigmentation.

of the northeastern Pacific, are inadequately known. In all probability the eggs of both species are found in gelatinous egg masses. Perhaps the larger egg masses belong to *S. alascanus*, which reaches a larger maximum size than *S. altivelis*. Since further study is needed to differentiate the eggs and larvae of these closely related species, the egg masses reported on here may belong to either or both species.

Our catches of *Sebastolobus* in bottom trawls indicate that these fish are most common along the continental slope, from 400–600 fathoms, their bathymetric distribution being generally deeper than that of *Sebastodes*, the multitypic scorpaenid genus with ovoviviparity. All the egg masses (Table I) were collected over the continental slope where the depth of water was 200–1000 fathoms. The dates of collection and the fact that all eggs, except those taken on March 30, were in advanced embryonic stages, suggests that spawning occurs between March and May.

Although other teleosts lay pelagic egg masses, such as some Lophiiformes and Ophidiidae, the only other fish known to spawn this type of egg along the Pacific coast of North America is *Scorpaena guttata*, another scorpaenid (Orton, 1955). *S. guttata* is a shallow-water form and is not found north of California, its extreme northern limit recorded as Monterey Bay (Phillips, 1957). The bilobed egg balloons of this species (Barnhart, 1937) are very similar to those reported herein. The eggs can be easily distinguished, however, as *Sebastolobus* eggs have a distinct oil globule and perivitelline space which is lacking in the eggs of *Scorpaena guttata*. The larvae of *Sebastolobus* can be distinguished from other scorpaenids on the basis of size and pigmentation. The pigmentation pattern of *Sebastolobus* larvae, with the melanophores localized on the somites between the vent and tail, differs markedly from that of the smaller *Scorpaena* larvae.

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Age of Young Sablefish, *Anoplopoma fimbria* (Pallas) 1811

Past ageing of sablefish (*Anoplopoma fimbria*) has been hampered by lack of small specimens which has prevented substantiation of calculated ages of young fish. For example, Pruter (1954) concluded that sablefish of approximately 31 cm (fork length) caught in the summer were in their second year, but he noted a suggestion of another "annulus" present in some scales between the focus and the narrow band of circuli which he considered as the first annulus. He suggested that his age interpretations could be one year too low if these were true annuli.

Opportunity to investigate this area of uncertainty was presented when small sablefish were captured during recent trawling off the northern coast of Oregon. On July 4 and 5, 1961, eight sablefish, smaller than previously aged, were taken in a trawl net off the northern coast of Oregon in 175 and 225 fathoms of water. One was caught July 4 in 225 fathoms at approximately Lat. 46°01′N, Long. 124°44′W; and seven were caught July 5 in 175 fathoms at approximately Lat. 45°00′N, Long. 124°45′W. The specimens were captured during deep-water marine explorations by the University of Washington, College of Fisheries' research vessel, M.V. *Commando*, chartered by the Exploratory Fishing and Gear Research Base, United States Bureau of Commercial Fisheries, Seattle, Washington.[1]

All the fish were blue–black on the dorsal surface and along the sides to approximately the lateral line where they were light blue in color. The ventral surface was white. All had the adult appearance and coloration except for the light blue along the sides. Kobayashi (1957), using a plankton net near the Aleutian Islands, captured larvae and young sablefish which ranged in size from 1.1–3.0 cm (total length), and Brock (1940), using a dip net near the surface of the ocean about 200 miles off the Oregon coast, reported catching young sablefish which ranged in size from 2.1–3.5 cm, standard length. Brock also reported that Gilbert in 1915 noted many small sablefish (7.5 cm in length) swimming in large schools near the surface in Monterey Bay, California. Since the specimens captured off the Oregon coast in 175–225 fathoms of water were from 12.3–16.4 cm in length, and because of their coloration and adult-like appearance, it can be theorized that sablefish first begin to assume adult behavior patterns at approximately six months of age and 12 cm in length.

The specimens obtained by the M.V. *Commando* were measured and scale samples examined for an indication of age. The following table shows the

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fork length in centimetres and the circuli count from the focus to the lateral margin of each scale:

Fork length	Circuli on scale
cm	*no.*
12.3	6
14.0	7
14.0	8
14.4	8
14.7	8
14.8	8
15.7	8
16.4	9

The scales, which were approximately 0.5 mm by 1.0 mm in dimension, showed no indication of having an annulus and therefore were believed to have been in their first year of growth or approximately six months of age. If sablefish spawn during the winter months (Thompson, 1941; Bell and Gharrett, 1945), this would seem valid since the specimens were captured in July. The scale radii of the small sablefish were approximately 0.75 cm measured from the focus to the anterior margin. Pruter (1954) showed that the scales and body of sablefish ranging in size from 30–90 cm grew at approximately proportional rates for the period of life covered by his samples. Projecting his regression line to fish smaller than included in his samples suggests that a 15-cm fish would have a scale radius of 0.75 mm. Pruter calculated the length range of one-year-old male sablefish to be between 23 and 43 cm and one-year-old females to be between 21 and 48 cm which would leave "0" age fish to be between 0 and 21 or 23 cm.

To further investigate the age of small sablefish, larger specimens were obtained during a subsequent cruise off the northern coast of Oregon, and from Mr Frank Haw, Washington Department of Fisheries. The latter samples were taken from the Puget Sound sport fishery. On December 2, 1961, two sablefish, 26.0 and 32.4 cm (fork length) were caught off the Columbia River in 50 fathoms of water and kept for age analysis. There were 14 and 16 circuli, respectively, on scales examined from each fish, and scales from both specimens showed what appeared to be the first annulus forming on the outer edge. The six sablefish lengths and scales obtained from Puget Sound on December 9, 1961, ranged in length from 26–30 cm (fork length). Scales examined from these fish showed more than 15 circuli on each scale with the first annulus forming on the outer edge.

One-year-old sablefish examined in this study were of similar lengths to those noted as one-year-old fish by Pruter (1954). Since the eight smallest fish taken in July showed no trace of an annulus on their scales, it is believed that the first annulus is formed at a minimum length range of approximately 21–23 cm.

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4: 619 (blood pH and mortality in)
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6: 1105 (of Greiner Lake, Victoria Island, N.W.T.)
Ricker, William Edwin
4: 531 (growth and mortality of sockeye)
Roberts, Eve
2: 321 (dogfish gelatin)
Ronholt, Lael Lee
6: 1167 (range extensions for two species of caridean shrimps)

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Saanich Inlet, B.C.
1: 1 (oceanography of)
Sablefish (*Anoplopoma fimbria*)
6: 1175 (age determination of young)
Salinity (*see also* Oceanography)
1: 45 (and temperature structures in approaches to Vancouver Island)
5: 975 (and temperature in Quoddy Region)
Salmon, Atlantic (*Salmo salar*)
4: 625 (observations on behaviour)
Salmon, chinook (*Oncorhynchus tshawytscha*)
5: 851 (seasonal changes in feeding in British Columbia waters)
Salmon, coho (*Oncorhynchus kisutch*)
5: 851 (seasonal changes in feeding in British Columbia waters)
6: 1047 (behaviour of juveniles related to migration)
Salmon, Pacific (*Oncorhynchus* spp.)
1: 137 (visible migrations of adult)
4: 561 (estimations of ocean mortality rates)
6: 1025 (respiratory metabolism)
Salmon, sockeye (*Oncorhynchus nerka*)
2: 327 (olfactory perception—response to food extracts)
4: 531 (ocean growth and mortality)
4: 619 (blood pH and mortality in)
Salted fish
3: 437 (coliform bacteria in light salted fish brines)
Scallop (*Placopecten magellanicus*)
5: 877 (possible effects of Passamaquoddy power project on)
Scorpaenidae (*Sebastolobus*)
6: 1169 (embryological and larval development)
Scott, David Paul
1: 149 (radioactive caesium as a fish mark)
4: 715 (food and fecundity of trout)
Scott, William Beverley
6: 1013 (longjaw cisco in Lake Erie)
Sculpin (*Cottus bairdi*)
6: 989 (carrier of furunculosis)
Seal, harp (*Phoca groenlandica*)
5: 839 (air blowing of oil)
Sebastolobus
6: 1169 (embryological and larval development)
Sehdev, Harcharan Singh
4: 619 (blood pH and mortality in trout and salmon)
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2: 363 (first recording from British Columbia)
Shark, white-tip (*Pterolamiops longimanus*)
3: 517 (occurrence near Georges Bank)
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1: 101 (factors affecting shellfish toxicity at Head Harbour, N.B.)
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5: 877 (possible effects of Passamaquoddy power project on)
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6: 1167 (range extension in northeastern Pacific)
Sinclair, Alexander Campbell
1: 127 (glycogen in trout tissues)
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2: 173 (rainbow trout)
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4: 625 (use in observing behaviour of Atlantic salmon and brook trout)
Smith, Stanford Henry
6: 1013 (longjaw cisco in Lake Erie)
Southcott, Burnett Anne
4: 615 (effect of antibiotics on fish quality tests)
Southward, Glen Morris
2: 335 (photographing halibut otoliths)
2: 339 (calculating halibut lengths from otoliths)
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1: 113 (longnose sucker of Great Slave Lake, N.W.T.)
2: 173 (rainbow trout in Loon Lake, B.C.)
5: 985 (relationship between growth, hatching, and spawning season in Atlantic herring)
Squires, Hubert Jacob
4: 677 (decapods in Frobisher Bay)
5: 891 (blue ling from Newfoundland)
Stevenson, James Cameron
5: 735 (survival of herring larvae)

Stewart, Kenneth William
6: 1161 (morphology and optical properties of the adipose eyelid of fishes)
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1: 113 (growth and reproduction)
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5: 735 (Pacific herring larvae)
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4: 635 (herring)
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6: 1143 (analysis of length distribution)
Tanaka, Syoiti
4: 521 (effect of reduction of fishing effort)
6: 1143 (analysing polymodal distributions)
Tarr, Hugh Lewis Aubrey
3: 519 (phosphorus compounds and sugars in fish muscle)
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3: 401 (anatomical comparison of king crab with closely related species)
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1: 45 (and salinity structures in approaches to Vancouver Island)
5: 975 (and salinity in Quoddy Region)
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3: 445 (cod tagging in the Newfoundland area)
5: 811 (oceanic puffer from Newfoundland)
5: 891 (blue ling from Newfoundland)
Thomson, John Arthur Collingwood
3: 497 (fecundity of Pacific cod)
Thurston, Claude Elmore
1: 39 (physical and chemical data on lake trout)
Tibbo, Simeon Noel
3: 517 (new records for occurrence of whitetip shark and dolphin)
5: 981 (young herring in captivity)
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5: 895 (electromagnetic measurement in passages of Passamaquoddy Bay)
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6: 1005 (temperature and digestion by bass)
Tomlinson, Neil
2: 321 (dogfish gelatin)
2: 327 (olfactory perception in juvenile salmon)
4: 619 (blood pH and mortality in trout and salmon)
4: 733 (phospholipid content of lingcod)
6: 997 (glycogen in fish muscle)
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6: 1121 (north Pacific Ocean)
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Trites, Ronald Wilmot
5: 895 (electromagnetic measurement of tidal flow)
5: 975 (temperature and salinity in the Quoddy Region of Bay of Fundy)
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6: 1095 (enzymic digestion of cod)
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1: 149 (marked with radioactive caesium)
4: 625 (observation on behaviour)
6: 989 (carrier of furunculosis)
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1: 39 (physical and chemical data for two subspecies)
6: 1085 (relative efficiency of nylon and cotton gill nets in fishing)
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2: 173 (spawning runs)
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4: 715 (effect of food on fecundity)
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Truscott, Beryl
6: 1095 (cod tropomyosin)

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1: 45 (temperature and salinity structures in approaches to)
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6: 1105 (relict fauna of Greiner Lake)

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6: 1095 (cod tropomyosin)
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6: 1163 (amphipods in low-oxygen marine waters)
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4: 687 (distinctions between *Coregonus nasus* and other whitefishes)
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6: 1121 (effect on ocean circulation)
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1: 169 (fat hydrolysis in frozen lingcod and gray cod)

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4: 521 (effect of reduction of fishing effort on)
4: 531 (of sockeye salmon in high-seas and inshore fisheries)

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3: 377 (of Foxe Basin)
4: 657 (quantitative estimations off Washington and British Columbia)